



Dynamic modelling in the scope of biological invasions research and management

Ana Buchadas

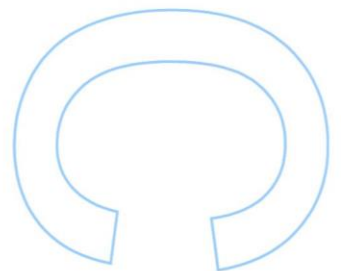
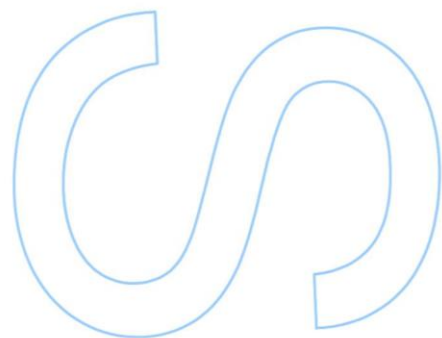
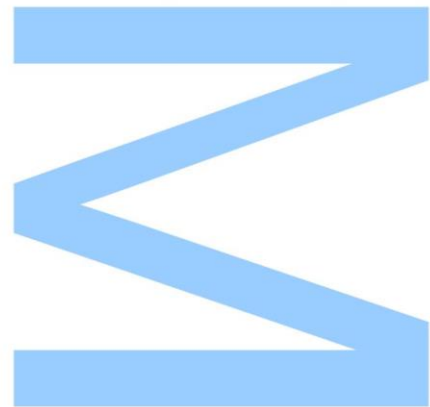
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Todas as correções determinadas
pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, ____/____/____

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Foreword

This study has already been presented as an oral communication on:

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Abstract

Invasive alien species are increasing in number, extent and impact worldwide, constituting a phenomenon which may lead to important ecological, economic, and social impacts. These species can modify the structure and functioning of ecosystems thus having implications on native biodiversity and ecosystem services. The need to address biological invasions and their impacts has fostered an increasing commitment from the society, politicians and stakeholders to manage invaded ecosystems. Putting forward efficient management plans is, nonetheless, a massive socio-ecological challenge.

Integrating the spatial-temporal dynamics inherent to the invasion process in management planning is a rather promising research approach to tackle this challenge. The inclusion of dynamic processes in ecological modelling frameworks (i.e. dynamic or hybrid models) adds up a temporal-explicit dimension to the understanding, prediction (current conditions) and forecasting (future conditions) of invasion processes, offering high potential for multi-scale optimization of management actions. However, the extent to which dynamic approaches have been used for that purpose hasn't yet been fully explored.

Based on an extensive literature review, we examined the extent to which dynamic modelling has been applied to address biological invasions worldwide. We also assessed how dynamic modelling has evolved along time regarding management strategies for invasions.

Our results show that modelling approaches, and specifically dynamic modelling techniques, have been increasingly pursued in the scope of invasion biology. Particularly we found that dynamic modelling application for invasion management presented a biased application regarding both geographical and taxonomical focuses. Moreover, we shown that dynamic modelling has been predominantly applied to support the management of invasive species, especially at local scales.

Finally, we highlight that the combination of dynamic with static modelling approaches, i.e. hybrid models with spatially-explicit outputs, can be the most adequate solution to support early stages of management such as prevention, and to improve and optimize the monitoring of invasion processes. Furthermore, developing and testing hybrid models must be considered as a priority in invasion research, aiming to manage invasions across spatio-temporal scales.

Keywords

biological invasions, dynamic models, hybrid models, literature review, management, static models

Resumo

As espécies exóticas invasoras têm vindo a aumentar nos vários locais do planeta, tanto em número, extensão, como em impactes causados, constituindo um fenómeno potencialmente nefasto com consideráveis impactes aos níveis ecológico, económico e social. As espécies invasoras possuem a capacidade de alterar a estrutura e funcionamento dos ecossistemas, podendo promover consideráveis transformações, tanto na biodiversidade nativa como nos serviços de ecossistema associados. Com este reconhecimento, surgiu a necessidade de abordar mais seriamente tanto as invasões biológicas como os seus impactes, levando a um maior compromisso por parte da sociedade, políticos e gestores. Mesmo com este compromisso assumido, a capacidade de criar planos de gestão eficientes tem-se mostrado até à atualidade, um grande desafio sócio-ecológico.

Para a resolução deste desafio têm surgido abordagens promissoras, como é o caso da integração das dinâmicas espaço-temporais, inerentes aos processos de invasão, nos planos de gestão. A inclusão destes processos dinâmicos pode ser feita através de abordagens de modelação ecológica, com recurso a modelos de carácter dinâmico ou híbridos, permitindo tanto introduzir uma dimensão temporal explícita à compreensão e previsão dos processos de invasão, como potenciar uma otimização dos esforços de gestão a múltiplas escalas. No entanto, a quantificação da aplicação destas abordagens dinâmicas para gestão de espécies invasoras ainda não foi feita.

Com base numa extensa revisão de literatura, quantificámos o grau de aplicação das abordagens dinâmicas para abordar questões relacionadas com invasões biológicas a nível global. Avaliámos também a evolução temporal dessa aplicação, especificamente para problemas relacionados com a gestão de invasões.

Os resultados permitem perceber que a modelação ecológica, especificamente abordagens com carácter dinâmico, têm sido cada vez mais utilizadas no âmbito dos estudos em invasões biológicas. Em particular, a aplicação de modelação dinâmica para a gestão de espécies invasoras mostrou ser enviesada nos estudos revistos relativamente aos focos taxonómico e geográfico. Também foi possível verificar que a modelação dinâmica tem sido a técnica mais aplicada no apoio a medidas de gestão de espécies invasoras, especialmente à escala local.

Por fim destacamos que a combinação de abordagens de modelação dinâmica com abordagens estáticas, ou seja, a utilização de modelos híbridos, (tipicamente com carácter espacialmente explícito) poderá ser a solução mais indicada ao combate das fases iniciais das invasões biológicas, especificamente na prevenção e na criação e otimização de redes

de monitorização. Com base nas conclusões obtidas neste estudo, consideramos que deve ser dada prioridade na investigação deste tema ao desenvolvimento e validação das abordagens híbridas, de forma a se conseguir uma eficiente gestão tendo em conta as diferentes escalas espaciais e temporais associadas a este processo.

Palavras-chave

Gestão, invasões biológicas, modelos dinâmicos, modelos estáticos, modelos híbridos, revisão de literatura

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List of abbreviations

GNI – Gross National Income

HSM – Habitat suitability model

IBM – Individual-based model

INI – Introduction-naturalization-invasion continuum

IPPC – International Plant Protection Convention

ISI WOS – ISI web of Science

IUCN – World Conservation Union

OIE – World Organization for Animal Health

PCA – Principal component analysis

PICO – Population-Intervention-Comparison-Outcome

SCOPE – Scientific Committee on Problems of the Environment

UE – European Union

1. Introduction

1.1. Invasive Species

Definition and associated concepts

Invasive alien species (hereafter “invasive species”) have been increasing in number and extent over the past half century, triggering escalating impacts worldwide (McNeely et al., 2001, MA 2005, Pyšek and Richardson, 2010, Vilà et al., 2010, Simberloff et al., 2013, Fei et al., 2014, Tassin and Kull, 2015). Along with other threats, as habitat change and overexploitation, environmental pollution and climate, we are perceiving increased ecosystems modifications (MA, 2005). Biological invasions have been contributing to the homogenization of biodiversity and are regarded as one of the major causes to the decline of biodiversity translating into reduced ecosystem services provision worldwide (McGeoch et al., 2010, MA, 2005). Due to the increasing rates of invasion, both in number and frequency of novel and ongoing invasions, attributed to growing trade and faster transportation (Westphal et al., 2008, Humair et al., 2015), invasion ecology has become an imperative topic in ecological studies.

Invasive species can be defined as a subset of alien species, species intentionally or unintentionally transported by humans to new geographic areas overcoming biogeographical barriers; that become naturalized and are able to maintain self-replacing populations producing reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and that finally have the potential to spread over long distances (Richardson et al., 2000, 2010b). The process of invasion can be described by different phases of invasion in an introduction-naturalization-invasion continuum (INI) (Fig. 1). The definition of Invasive species can also implicate the presence of a perceived impact. This definition, supported by the World Conservation Union (IUCN) and the Convention on Biological Diversity and the World Trade Organization, explicitly assumes that invasive species must cause perceived impacts to the economy, environment or health (see IUCN 2000). In the scientific community this type of impact-definition is rather controversial as, some invasive species may not cause perceived impacts only due to low residence time (Richardson et al., 2000, Rejmánek et al., 2002, Ricciardi and Cohen, 2007).

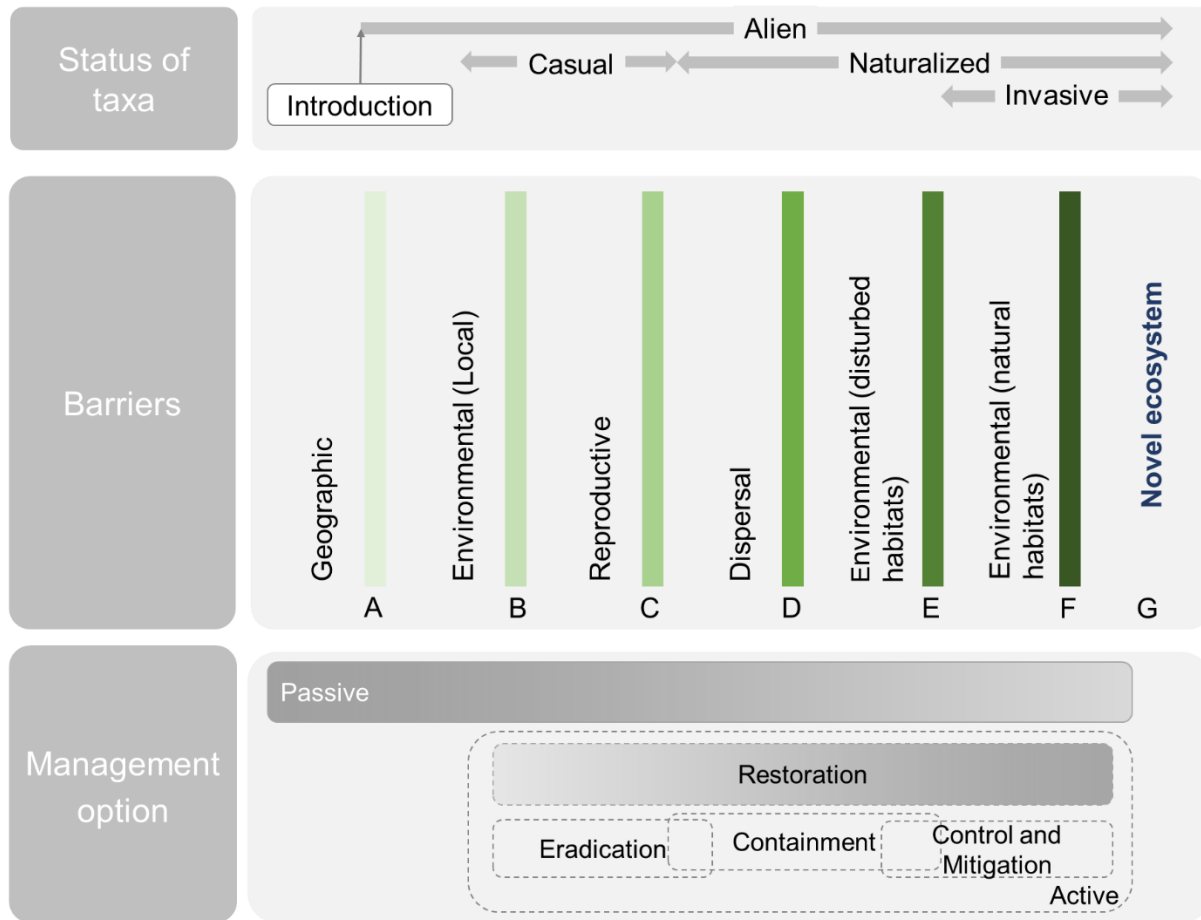


Fig. 1 - Schematic representation of the introduction-naturalization-invasion continuum status (INI) of the species introduced, the general barriers limiting its spread, and management options associated. The barriers to overcome are: (A) geographical, (B) Environmental (abiotic and biotic) at the site of introduction, (C) Reproduction (ability to create offspring), (D) Local/regional dispersal, (E) Environmental conditions in human-modified or alien-dominated areas, and (F) Environmental conditions in natural or seminatural areas. If changes in ecosystem processes, structure and function occurs, a novel ecosystem can arise (G). Management options can be related with each status of taxa and barriers, in a solid outline box are represented the passive options (prevention, risk analysis, monitoring) – more frequently applied in early stages of invasion or even before introduction -, and in dashed outline are represented the active management options (eradication, control, mitigation and restoration – more efficient at early stages of invasion) considered in this study - based on Richardson et al. (2000), Hulme (2006) and Marchante (2011).

As a research field, invasion ecology has been established since Elton's 1958 monograph "The Ecology of Invasions by Animals and Plants", being Elton considered the father of invasion ecology (Richardson and Pyšek, 2008, Simberloff, 2010). Much work since then has been developed to explain why invasive species thrive. 1982's programme on the ecology of biological invasions of the Scientific Committee on Problems of the Environment (SCOPE, an arm of the International Council of Scientific Unions) put forward three questions that would remain unanswered till these days, constituting the main topics in invasion ecology and pushing invasion ecology as a discipline. Such questions are as follow: 1 "What factors

determine whether a species becomes an invader or not?"; 2 "What site properties determine whether an ecological system will resist or be prone to invasion?"; 3 "How should management systems be developed to best advantage, given the knowledge gained from studying questions 1 and 2?". Currently, we consider that questions 1 and 2 are related respectively with invasiveness and invasibility, two main concepts in invasion ecology. Invasiveness can be defined as the ability of a species to become invasive, and relies on identifying particular traits that are consistently associated with the tendency of species to invade (Reichard and Hamilton, 1997) and invasibility relates with the features of the environment (e.g. landscape structure and composition) that allows and promotes the invasion (for more details, see Richardson and Pyšek 2006). The concept of invasibility can also be related with the communities, being the community invasibility dependent of the level of resources available at the time of invasion (resource fluctuation hypothesis, see Davis et al., 2000), on the presence of key species as antagonist (Biotic resistance hypothesis) or facilitators (invasion facilitation hypothesis) acting respectively as constraining or facilitating the establishment of new species (Inderjit et al., 2005). Many other hypotheses have been developed to address invasiveness and invasibility (see Inderjit et al., 2005) therefore the knowledge about the invasion process has substantially improved (Richardson and Pyšek 2006, Davis 2009). However, the main findings rely on the fact that invasions are context specific, being difficult to generalize invasion concepts. For instances, traits that contribute to the success of taxa as invasive aliens are not universal and need always to be related with the features of the invaded ecosystem as community composition, geographical conditions, and a set of external factors, including propagule pressure (i.e. the number and frequency of introductions of a given species; Richardson and Pyšek, 2006)

Ultimately, to go further answering the SCOPE programme questions, a more holist approach, focused on the concept of invasion syndrome – a typical recurrent associations of species biology and invasion dynamics with particular invasion contexts such as an invasion stage, invaded habitat and/or socioeconomic context (Kueffner et al 2013) – is required.

Impacts

The introduction of a new species to a given environment can promote modifications on the structure or functioning of the system (Pyšek and Richardson, 2010, Gaertner et al., 2014). This alteration (commonly called impact) may be manifested at different levels of organization, from the organism (e.g., effects on mortality and growth of a given individual), populations (abundance, genetics), communities (species richness, evenness, composition, trophic

structure), ecosystems (physical habitat, nutrient cycling, contaminant cycling, energy flow) or at region level (species richness, beta diversity; Pyšek and Richardson, 2010, Ricciardi et al., 2013). Meanwhile, the perception of impacts may be modulated by the spatial and temporal scale of perception (Strayer et al., 2006, Powell et al., 2011, 2013, Ricciardi et al., 2013, Kumschick et al., 2014), for instance, the impact of invasive species with large home ranges (e.g., vertebrates) might be spatially diluted and challenging to quantify at the local scale (Kumschick et al., 2014).

Alien species have, for the most part, little or no detectable effects on the new environments (Pyšek et al., 2012, Kumschick et al., 2014) having often positive effects on various ecosystem services, as provisioning of food and fiber; regulating the spread of human diseases; and providing aesthetic, recreational, and tourism benefits (Pejchar and Mooney, 2009, Kettunen et al., 2009, Blackburn et al., 2014, Bonanno, 2016). Moreover, alien species can be favourable to native biodiversity by, for example, providing habitat and food resources to rare species (Chiba, 2010, Schlaepfer et al., 2011). Nevertheless, only a rather small proportion of alien species evolving to invasive species promote known negative impacts. It is important to notice that there is an open scientific debate and some justified criticism on how impact is currently being evaluated, a “good” or “bad” impact is not an objective way to accurately depict invasive species impacts (see Pyšek et al., 2012, Simberloff et al., 2013). Still, invasive species have been often considered as harmful to ecosystem services, disrupting human well-being and threatening biodiversity (MA, 2005, Pejchar and Mooney, 2009, Vilà et al., 2010, Pereira et al., 2012). Between the well-known ecosystem services negatively impacted we can state the following: supporting services (by modifying soil and sediments, nutrient cycling, and primary production, etc.), provisioning services (by promoting loss of food resources, fuel or fiber, threatening endangered native species or altering genetic resources), regulating services (by changing pollination, altering erosion regimes, water regulation and purification, etc.) or cultural services (by changing the perception of the landscape context, etc.; Vilà et al., 2010). Changes promoted by invasive species can be direct and indirect, and may act in subtle or poorly studied interactions that can yield to unknown substantial effects over time (Ricciardi et al., 2013, Blackburn et al., 2014). A small proportion of invasive species, named transformers (*sensu* Richardson et al., 2010b) can alter ecosystem processes by a wide variety of mechanisms across spatial and along temporal scales, and over a wide range of degree of impact (Ehrenfeld, 2010). The transformer species can rely on mechanisms as ecosystem engineering (a species that alters resource availability for the native species through nontrophic behaviours), by acting as keystone species (promoting an effect on other species and/or on material fluxes out of proportion to its abundance, and through entirely biotic mechanisms) or acting as foundation species (creating a physical structure that determines

the physical characteristics of a given site over its abundance and/or particular characteristics; Ehrenfeld, 2010). The modifications on ecosystem processes promoted by invasive species may lead to reduce local diversity, alter ecosystem structure and function, and modify disturbance regimes, causing potential irreversible changes resulting on regime shifts (Ehrenfeld 2010, Bennett et al., 2005). Changes in ecosystem feedbacks due to invasions can facilitate further invasions (positive feedbacks) and amplify the invaders impacts on native communities, creating the called invasion meltdowns (sensu Simberloff & Von Holle 1999). All the presented modifications in the system can ultimately lead to the emergence of novel ecosystems, an 'ecosystems containing new combinations of species that arise through human action, environmental change, and the impacts of the deliberate and inadvertent introduction of species from other parts of the world' (see Hobbs et al., 2006).

The biological invasion disruption of ecosystem services is also well known to impact negatively on economy, sociology, culture, and human health (Pejchar and Mooney, 2009, Pyšek and Richardson, 2010, Vilà et al., 2010). Contrasting impact perceptions often arise from different actors (politicians, scientists, economists, etc.) since some impacts considered as negative from conservation perspective can be perceived as positive by other actors (e.g. timber production using monospecific alien stands plantations, Simberloff, et al., 2013).

The economic impacts related with biological invasions are astonishing, for example, in Europe costs were estimated to be at least €12.5 billion per year based on documented costs and probably over €20 billion per year when extrapolated to the area affected by invasive species, likely being underestimated (Kettunen et al., 2009). Evaluating economic impact is, nevertheless, a challenging task. One option, to evaluate the impact associated with invasion process, is to sum costs associated with losses of biodiversity and impaired ecosystem services, as well as the costs of managing invasive species (Pyšek and Richardson, 2010). To limit management costs, it's important to optimize management actions and create cost-effective analyses.

Management

Answering the third question posed in SCOPE 1982 programme, "How should management systems be developed to best advantage (...)" has proven to be a more complex task. When planning management actions, a comprehensive approach is needed. A management approach should consider the ecological impacts as well as the socio-economic impacts (Hulme, 2006, Pyšek and Richardson, 2010, Estévez et al., 2015). Moreover, when managing, it is required to fully understand the technical options available; the risks associated with each

option, the likelihood of success; and ultimately to increase the knowledge of the spatial dynamics of the invading species potentiating the management planning (Hulme, 2006, Pyšek and Richardson, 2010).

Key management options can be classified as: prevention, early detection and eradication, containment, control, mitigation and restoration (Hulme, 2006) the option depends on the invasive species position on the spectrum of introduction-naturalization-invasion (INI) continuum (fig. 1) and on abundance and extent of the species distribution (Wittenberg and Cock, 2001). In this study, we considered management options as passive management referring to preventive actions as risk analysis, quarantine, monitoring; and active management actions as direct or indirect actions applied to limit invasive species spread and impacts, as control, eradication, mitigation, etc..

Preventing the introduction of species with a high risk of becoming invasive is the most cost-effective management strategy (Wittenberg and Cock, 2001, Hulme, 2006, Pyšek and Richardson, 2010). Border control and quarantine measures are often the first opportunity to respond to invasive species incursions (Hulme, 2006). Prevention relies on risk assessment studies to evaluate invasive species threat and the likelihood of entry and establishment. Risk assessments are difficult to perform due to limitations on data availability (e.g. to determining invasiveness), and the inclusion of socio-political interests and values in these assessments (Pyšek and Richardson, 2010). Advances were made towards developing risk maps applying ecological modelling approaches to predict both invasive species spread and areas high risk of invasion, currently or in the future (Pyšek and Richardson, 2010). When prevention fails, and an invasive species establish eradication is the preferred course of action, early detection is crucial for the feasibility of eradication (Wittenberg and Cock, 2001, Simberloff, 2009), Hulme, 2006). Eradication actions involves removal of the whole invasive species population from a specific area. When eradication is not feasible, efforts must be targeted to limit the spread of the invasive species, containment, or/and to reduce the density and abundance of the invasive species to keep it below an acceptable threshold, this corresponds to the control option (Hulme, 2006). Within control options, the biological control option becomes the most cost-effective approach, since it can provide a permanent, self-sustaining and when there is a high specificity of the agents used is verified, ecologically safe approach (Wittenberg and Cock, 2001). Classical biological control aims to reduce the invasive species populations to ensure that the species no longer pose a significant problem on the ecosystem (Hulme, 2006, Pyšek and Richardson, 2010). Multiple approaches may be coordinated to optimize a management action, for instance, to contain and control a core population and eradicate outlying populations. Ultimately, if the control actions are just impossible to implement, due to

impracticability, inadequacy or being economically unviable the last available resource is to implement mitigation actions to minimise impacts (Wittenberg and Cock, 2001). Management options should always be integrated in a broader restoration frame to, not only, remove invasive species but simultaneously promote the re-establishment or reintroduction of native species and restore the ecosystem (Wittenberg and Cock, 2001). All management programmes considering invasive species should be followed by monitoring efforts in order to evaluate the level of success and rise the opportunity to modify and/or adapt the approach (Buckley, 2008). Occasionally, when the ecosystem presents an extreme level of alteration and/or the management is not possible, a “no action” option can be the best approach.

The need to tackle invasions and their impacts has fostered an increasing commitment of researchers and conservation planners to manage invaded ecosystems (Estevez et al., 2015, Rotherham and Lambert, 2012). The development of predictive tools to support knowledge, capacity and decision-making in the scope of invasion processes is therefore vital for the effectiveness of management actions and policies (Ameden et al., 2009, Vicente et al., 2013, 2016)

1.2. Ecological Modelling and Invasion biology

Ecological modelling as a tool to understand, predict and forecast

An ecological model can be defined as a synthesis of what we know about the ecosystem with reference to the considered problem, a model doesn't intend to represent the full system but only the essential features in the context of the problem to be solved or described (Jørgensen and Fath, 2011). Models may be physical, as a microcosm, conceptual or mathematical, describing the ecosystem in mathematical terms (Jørgensen and Fath, 2011). In this study, we only focus on mathematical models.

A model includes the knowledge on components interactions, on the processes, often formulated as mathematical equations, and the importance of the processes with reference to the problem (Jørgensen and Fath, 2011). To be able to understand such a complex system, as ecosystems, and, being just impossible to survey the multiple components and reaction in an ecosystem, ecological models can be very useful. Modelling allows the understanding, the prediction, and the forecasting of a system progress. Being a useful instrument to survey complex systems, to reveal system properties, to reveal gaps in our knowledge and set up research priorities, and to test hypotheses (Jørgensen and Fath, 2011). Being the purpose behind the use of models an iterative development of a pattern, as every time a hypothesis

tested is correct, another piece of the puzzle may be added. When the pieces of the puzzle are all together, mimicking the real process, they can have important applications on predicting and forecasting across space and/or along time the evolution of the system (Jørgensen and Fath, 2011).

Application of modelling techniques in ecology and types of models

Ecological modelling has in the last three decades undergone a fast development due to advances in computer technology, enabling the use of more complex models; an increase on environmental and ecological systems knowledge and a general understanding on environmental processes (Jørgensen and Fath, 2011).

Ecological modelling has been widely used across several ecological domains, such as eutrophication mitigation (e.g. Alvera-Azcarate et al., 2003), climate change impacts (e.g. Vicente et al., 2013), pollution effects (e.g. Hinojosa et al., 2008), national parks management (e.g. Miller and Urban, 2000), and as support to monitoring networks design (e.g. Amorim et al., 2014, Carvalho et al., 2015, Vicente et al., 2016). When properly calibrated and evaluated, and if applied with insight and with regard to their underlying assumptions, ecological models are able to simulate conditions that are difficult or impossible to understand otherwise (Jørgensen and Fath, 2011).

Therefore, efforts to comprehend and accurately predict the behaviour of a given system have resulted in the development of several modelling approaches suiting different modelling aims (Jørgensen and Bendoricchio, 2001). Among many classifications of modelling approaches (e.g. reductionistic/ holistic, deterministic/ stochastic, linear/ nonlinear, etc.), two major types of ecological models can be recognized, depending on their capacity to describe and analyse the nature of the processes by which a particular phenomenon is created (Hannon and Ruth, 2014): static models and dynamic models. Static models can be defined as models that represent a particular phenomenon in a given frame of time or at different independent points in time (i.e. comparative static models) (Hannon and Ruth, 2014). These are, typically, statistical based phenomenological models that relate observations of a response variable (e.g. species occurrences) with environmental variables or drivers (Guisan and Thuiller, 2005, Franklin, 2010). Static models, as the name implies, are models that relies in a static mathematical relationship between the occurrence of a given species and the environmental conditions. It assumes that the relationship remains across space and along time. Static models, for example habitat suitability models (HSM), are considered important screening tools in ecology (Gallien et al., 2010).

On the other side, dynamic models are based on ecological processes (i.e. process-based models), and differ from static models by explicitly incorporating time-dependent changes in the state of a system (Hannon and Ruth, 2014). Dynamic models may comprise various modelling approaches, such as biogeochemical dynamics models (e.g. Soetaert et al., 2000), population dynamics models (e.g. Kriticos et al., 2003), individual-based models (IBMs; e.g. Nehrbass and Winkler, 2007), and/or cellular automata systems (e.g. Crespo-Perez et al., 2011). Historically, examples of dynamic modelling approaches include the classical developments of Lotka-Volterra in the 1920s, the application of population dynamics models in the 1950s and of eutrophication models during the 1960s; more recently, IBMs and cellular automata, spatially explicit approaches, have seen their growth in the late 2000s and 2010s (Jørgensen and Fath, 2011, Chen et al., 2011, Jørgensen, 2008, Jørgensen, 1994).

Ecological modelling approaches to model invasion process and to support management options

In recent years, ecological models have been applied as tools to understand the key drivers of invasion processes (Neubert and Caswell, 2000, Vicente et al., 2010), to predict areas of potential distribution, and to forecast potential impacts of invasive species, under distinct social-ecological scenarios (Vicente et al., 2016, Peterson et al., 2008).

Static approaches, as HSMs, have been commonly used in invasion ecology (e.g. Peterson et al., 2003, Vicente et al., 2010). Nevertheless, static models fail to understand the processes and interactions underlying the respective ecological processes and their consequences (Gallien et al., 2010). Indeed, modelling invasive species range dynamics is particularly challenging since, by definition, these species usually constitute recent arrivals, thus not being in equilibrium with environmental conditions in the invaded region, and thereby violating one of the main assumptions of HSMs (Rouget et al., 2004). Contrastingly, dynamic models are able to overcome the limitations of static models and potentially allow for an easy analysis of multi-factorial management scenarios (Cuddington et al., 2013).

Still, the application of dynamic modelling in invasion ecology requires a deep understanding of the spatial-temporal dynamics of the invasion process (Gallien et al., 2010). In fact, the characteristics of the invasive species (i.e. invasiveness; Guisan and Zimmermann, 2000, Gallien et al., 2010), the features of the communities or landscapes under invasion (i.e. invasibility; Gallien et al., 2010), and the environmental variables that influence these processes (Gallien et al., 2010), are required for an accurate implementation of dynamic

models. Such requirements limit a broader implementation of this type of models in invasion ecology; still, the utility of dynamic models for conservation planning and management has been profusely highlighted (e.g. Thuiller et al., 2008, Franklin, 2010, Richardson and Whittaker, 2010, Cuddington et al., 2013) and recognized as the most appropriate technique to guide management decisions (Cuddington et al., 2013).

In this context, there is an increasing interest in hybrid models, i.e. coupling dynamic and static models (e.g. Santos and Cabral, 2004, Brook et al., 2009, Richardson et al., 2010a, Zurell et al., 2016). Such hybrid models allow integrating the predictive accuracy of static models, as phenomenological models at large spatial scales, and the ability to capture underlying process of dynamic models (Franklin, 2010, Gallien et al., 2010). Examples of coupled static-dynamic modelling can be found in the integration of HSMs and process-based models for management of invasive species. For example, Meier et al. (2014) coupled HSMs and population spread models to analyse the effectiveness of invasive species control actions for alternative cost scenarios and different management goals, and Richardson et al. (2010a) defined regions at high risk of invasion by coupling a cellular automata model with HSM.

1.3. Objectives

The extent to which dynamic models have been actually applied in the management of invasive species is still under-evaluated. Literature reviews allows to synthesize the extent of the literature on a topic of interest, and to address potential gaps (Paré et al., 2015). A review can be defined as a way 'To view, inspect, or examine a second time or again' (Grant and Booth, 2009). Specifically, review studies can assume an essential role on building knowledge, as well as on understanding the scope of a given topic of interest, providing a conceptual background for subsequent research (Paré et al., 2015). Review studies may also prioritize topics or domains for future research (Paré et al., 2015). Therefore, we performed an extensive literature review to analyse the extent, and the goals, to which dynamic modelling has been applied in support of analysing and managing biological invasions. We conducted a comprehensive review of published literature that applies dynamic modelling approaches in the study of invasive species and respective management.

To do so, two major goals were addressed (G) and four hypotheses were tested (H):

G1 – To examine the extent to which ecological dynamic modelling has been used to address biological invasions worldwide. To do so, we tested if (H1.1) ecological modelling, particularly

dynamic modelling, has been increasingly used in biological invasion studies; and (H1.2) specifically applied to support decision-making for biological invasion management (H1.2).

G2 – To understand how dynamic modelling approaches have evolved with time, regarding management strategies targeting biological invasions. To assess this goal, we analysed whether (H2.1) models and their applications have known improvements and upgrades (from dynamic to hybrid models, from non-cost to cost evaluation, and from non-spatially-explicit to spatially explicit approaches); and (H2.2) if the geographical focus and the taxonomical focus of the modelling studies have changed along time.

2. Methods

2.1. Analytical framework and workflow

Ecological dynamic modelling has been proposed as a complementary approach to static modelling to address and evaluate biological invasion management goals (Cuddington et al., 2013), and have proven to be a robust way to take into account the effects of management on invasions. In this study, a review framework supported by standard protocols was applied in order to assess the incidence of dynamic modelling in biological invasion studies, and specifically in the management goals. This allowed comparing different patterns and tracing an historical overview of the use of dynamic modelling in invasions studies. Furthermore, since literature reviews are grounded on the selection of keywords and the search of these in search engines (Higgins and Green, 2011), the accurate selection of keywords is fundamental when trying to fully cover a thematic. The possibility of finding keywords that are able to cover the publication on a thematic relies on the standardization of vocabularies. It is therefore crucial that denominations are standardized in order to facilitate bibliographic review tasks. In this direction, our results may provide highlights concerning how to deal with keywords and abstract writing, overcoming several problems for review and synthesis research. The analytical workflow was organized around the two general major goals (G1, G2; see Fig. 2, Table 1). Under each of these two goals, two hypotheses were tested (H1.1 and H1.2 for G1; H2.1 and H2.2 for G2), as outlined above. For the second goal, additional sub-hypotheses were tested (Fig. 2– Literature Review, Table 1).

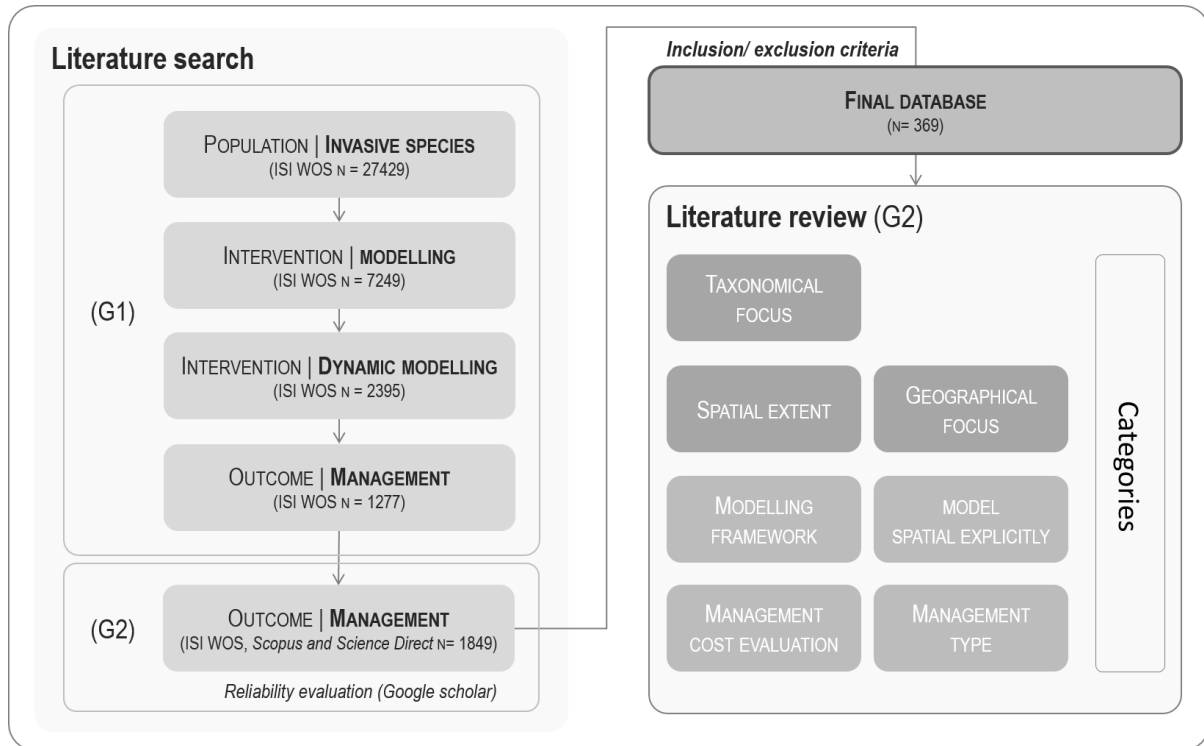


Fig. 2 - Analytical framework and workflow. The Literature search considered sequential hierarchical searches (ISI WOS) focused on Invasive species (Population), Modelling (Intervention), and Management (Outcome) keywords for Goal 1 (G1) and a combined search in ISI WOS, Scopus and Science direct for Goal 2 (G2). Records from combined search engines were selected based on inclusion/exclusion criteria (see Inclusion/exclusion criteria in section 2.4). The publications of the final database were individually reviewed (Literature review) and classified accordingly in seven categories, in order to address each sub-hypothesis related with Goal 2 of the study (see also Table 1).

Table 1 - Goals of the study, hypotheses and sub-hypotheses (related with the categories presented in Fig. 2) with their ecological rational and the respective scientific references.

Goals	Hypotheses	Sub-hypotheses	Rationale	Supporting references
G1. To examine the extent to which ecological dynamic modelling has been used to address biological invasions worldwide	H1.1: dynamic modelling has been increasingly used for biological invasion studies	-	Since they provide more in-depth understanding of invasion processes.	Sutherst and Bourne (2009), Vaclavik and Meentemeyer (2012)
	H1.2: dynamic modelling has been increasingly used for studies on management of biological invasion	-	Since they are recognized as the appropriate approach to guide management decisions.	Richardson and Whittaker (2010), Cuddington et al. (2013)
G2. To understand how dynamic modelling approaches have been evolved along time regarding management strategies targeting biological invasions	H2.1: incidence of the research geographically and taxonomically changed along time	H2.1.1 from taxonomic groups with impacts well known to a more general species selection H2.1.2 from continents with a longer history of research in invasion biology to more general areas; H2.1.3 from local and regional extent to global studies;	Since invasive process were firstly noticed and engaged where there was a significant economic/health impact and where they were more approachable/easier to study.	Perrings et al. (2010), Sutherst (2014), Pysek et al. (2008)
	H2.2: the application of dynamic modelling for management of invasive species has shown a transition along time	H2.2.1 From a uniquely dynamic model to application of hybrid models, combined with static species modelling H2.2.2 From a no cost evaluation to a cost evaluation of management options; H2.2.3 Between the chosen types of management options H2.2.4 From not spatial explicit to spatial explicit modelling approaches	Since there have been developments in dynamic modelling allowing for an improved application of these methodologies.	Hannon and Ruth (2014), Costanza and Ruth (1998)

2.2. Literature search

In order to address our goals, hypotheses and sub-hypotheses (Table 1), a literature review was performed on publications in which dynamic modelling approaches were applied to address invasive species and related phenomena, and then to support biological invasions management. The selection of the keywords was structured and built around a Population-Intervention-Comparison-Outcome (PICO) framework, suitable for searching terms into thematic groups and to identify publications for a throughout literature review (Higgins and Green, 2011) (Fig. 2).

An initial list of potential keywords, for the four Population-Intervention-Comparator-Outcome (PICO) components, has been built grounded on a list of articles of reference on the topics (Table 2) and a team of researchers specialized on modelling and managing invasive species. The initial potential keywords were iteratively tested on ISI web of Science database (ISI WOS) and further by adding new potential keywords identified during the literature search.

Throughout the search string, the keywords within each PICO components (P,I,C,O) were first combined using the boolean operator¹ "OR" and then the PICO main components were combined using the "AND" operator. Truncation and wildcards² symbols (denoted by *) were used to find alternative word endings (e.g. simulat*). Each term was added hierarchically, by apparent suitability, and for each term added, the first 10 references in the results were evaluated regarding the relevance for this study (ISI WOS results compatibility with the focus of the PICO components). Given that different authors use slightly different phrasing and diverse keywords, we selected the most-commonly and unequivocal keywords that we could found (see Table 2, for the final list of key-words).

¹ Boolean operator are simple words (AND, OR, NOT or AND NOT) used as conjunctions to combine or exclude keywords in a search

² Wildcards symbols are single characters, such as an asterisk (*), that are used to represent unknown characters or an empty string.

Table 2 - Keywords and consulted references for their selection for each PICO component, Population (Invasive species-related terms), Intervention 1 (Modelling-related terms), Intervention 2 (Dynamic-related terms) and Outcome (management-related terms).

Component	Population	Intervention 1	Intervention 2	Outcome
Thematic	Invasive species-related terms	Modelling-related terms	Dynamic-related terms	Management-related terms
Keywords	<i>"Ecolog* invasion*"</i> OR <i>"Biolog* invasion*"</i> OR <i>"Invasion biology"</i> OR <i>"Invasion ecology"</i> OR <i>"Invasive species"</i> OR <i>"Alien species"</i> OR <i>"Introduced species"</i> OR <i>"Non-native species"</i> OR <i>"Nonnative species"</i> OR <i>"Nonindigenous species"</i> OR <i>"Non-indigenous species"</i> OR <i>"allochthonous species"</i> OR <i>"Exotic species"</i> OR <i>"Released species"</i> OR <i>"Escaped species"</i> OR <i>"Invader"</i>	<i>"model*"</i> OR <i>"simulat*"</i> OR <i>"predict*"</i>	<i>"Dynamic*"</i> OR <i>"Mechanistic"</i> OR <i>"Temporal"</i> OR <i>"spat*-tempo*"</i> OR <i>"spat*tempo*"</i> OR <i>"space-time"</i> OR <i>"spat* and tempo*"</i> OR <i>"space and time"</i> OR <i>"time and space"</i>	<i>"manag*"</i> OR <i>"*control"</i> OR <i>"eradicate*"</i> OR <i>"containment"</i> OR <i>"mitigate*"</i> OR <i>"restor*"</i> OR <i>"monitor*"</i> OR <i>"prevent*"</i> OR <i>"risk analys*"</i> OR <i>"early detect*"</i> OR <i>"risk assessment"</i>
References	Pysek (1995), Richardson et al. (2000)	Guisan (2000), Jorgensen and Fath (2011)	Costanza and Ruth (1998), Gallien et al. (2010), Jorgensen and Fath (2011), An et al. (2015), Neuwirth et al. (2015)	Hulme (2006), Nentwig (2007)

The time span of our search was 1900-2014. Searches were carried out from October to November 2015, and were updated in March and April 2016. The search engines considered for our search were ISI Web of Science (ISI WOS; <http://webofknowledge.com/>), Scopus (<https://www.scopus.com/>) and Science Direct (<http://www.sciencedirect.com/>). To address the first goal, only ISI WOS search engine was used and no further evaluation or exclusion criteria were applied. ISI WOS was selected as it has been designed with the intention of satisfying users in citation analysis and although Scopus includes a more expanded spectrum of journals than ISI WOS, the citation analyses is limited to recent article when compared to ISI WOS (Falagas et al., 2008). The records retrieved by our search for G2 were combined and analysed to eliminate duplicates (total number of records, $n = 1849$), using EndNote x 7.4 (Thomson Reuters, 2013).

2.3. Evaluation

To evaluate the reliability of our search, the first 50 records retrieved by Google Scholar (using the main keywords “invasive species” AND “model” AND “dynamic” AND “management”) were compared with the resulting combined database (Fig. 2; following the procedures from Higgins and Green, 2011). The records from Google Scholar that were absent from our database (corresponding to 16% of the suitable records retrieved) were added, resulting in a final database of 1852 records (Fig. 2).

2.4. Inclusion/exclusion criteria

The resulting combined database was submitted to inclusion/exclusion criteria in order to remove irrelevant records (e.g. topics such as invaders from outer space- aliens; see

Table 3, for more information) and to obtain the final database (Fig. 2 – Final database). These criteria were then applied by individually checking the title, keywords and abstract of each record. In case of doubt, the full text of the record was reviewed afterwards (Fig. 2). Since two reviewers performed the application of the inclusion/exclusion criteria, the consistency of results was assessed through kappa statistics on 10 % of the database, resulting in a good consistency (kappa = 0.8; see Higgins and Green, 2011 for details).

Table 3 - Inclusion and exclusion criteria applied to the full database.

Criteria application	Exclusion criteria	Inclusion criteria
Type of record	Biographical items; corrections/corrigendum; items about an individual: poetry or anonymous documents which could not be found for checking veracity.	Research articles; book chapters; book reviews; editorial material; letters; meeting abstracts; news items; notes; paper proceedings; reviews, or forum papers.
Population	Records which focus on exotic/alien species in relation to space (mostly in astronomy, astrophysics and physics); alien species linked to literature and films with no connection to the real world; human population considered alien species (e.g. woman as an alien species; mostly from literature and movies); invasive species from a lyric perspective and attributed to human population (mostly religious and philosophical studies); clinical terms which use alien/exotic species for referring to an organism outside the human body (mostly in dentistry, ophthalmology, dermatology, oncology) or animals in laboratory experiences (clinical laboratory).	All records unless otherwise stated in the exclusion criteria.
Intervention	Records which do consider any type/technique of dynamic modelling to evaluate biological invasions (as defined above).	Records in which any type of dynamic modelling is considered to describe and analyse processes underlying biological invasions, attempting to capture changes in such processes in real or simulated time periods.
Outcome (not considered in the first step of the analytical framework)	Records which do not focus on the management of biological invasions, that focus on the outcomes of management actions for native species conservation, or focus on understanding invasion dynamics when not with the clear purpose of management.	Records that apply dynamic modelling for managing biological invasions, including: control, eradication, containment, mitigation or restoration, as well as monitoring, prevention and risk assessments.

The full text of each individual record from the final database (n = 369) was then reviewed and classified according to the categories shown in Table 4 (Fig. 2 - Literature Review).

Table 4 - Hypotheses, categories/questions, and classes to assess how dynamic modelling approaches have been used along time regarding biological invasions management strategies (Goal 2).

<i>Hypotheses</i>	<i>Categories / Questions</i>	<i>Classes</i>
<i>H2.1 Taxonomical group and geographic area</i>	Taxonomical focus What is the taxonomical group of focus?	Plant Invertebrate Vertebrate Other Not specified
	Geographical focus What is the targeted study area?	Global Europe South America North America Africa Asia Oceania Antarctica No reference
	Spatial extent What is the spatial scale of the study?	Global (multiple continents) Regional (within one continent but in multiple countries) Local (within one country) No reference
	Modelling framework Is the modelling approach a combination of dynamic approach with a species static model?	Not combined with a species static model Combined with a species static model
<i>H2.2 Characteristics of the modelling approach</i>	Model spatial explicitly Is the modelling approach spatially explicit?	Yes No
	Management type What management options and type, if passive (P) or active (A), were considered? (Passive management referred to preventive actions, and active management meant direct or indirect actions applied at invasive species post establishment.)	Risk assessment - P Preventing - P Monitoring - P Control - A Biological control- A Eradication - A Containment - A Mitigation - A Restoration - A Other No reference
	Cost evaluation Was a management cost evaluation done?	Yes No

2.5. Data analyses

Temporal trends of published records

A descriptive statistical analysis was performed to illustrate the temporal trends of published records in each step of the literature search (Fig. 2– Literature search, G1), and for each

category considered in the literature review (Fig. 2– Literature review, G2). The analyses were performed by plotting the total number of records published by year, and by assessing the proportion of records from the distinct categories (expressed as percentage) published in a given year. Analyses were first considered for the database extracted from ISI WOS (Fig. 2- Literature search, G1), and then for the final database (Fig. 2- Literature review, G2). The outcomes were presented as line (smoothing curves showing averages for 2-year time periods) or/and as column plots, for the time period between 1904 (first record retrieved by our search) and 2014 (see Results section).

Characterization of modelling publications in the scope of invasive species management

For the final database (see Fig. 2), a multivariate analysis was applied in order to evaluate the variation of the distinct categories in the ordination space. For a simplified illustration, two Principal Components Analyses (PCA) were applied to highlight the main gradients underlying variations in the distinct categories of published records, and to evaluate and visualize the main relationships between such categories. The first PCA considered the categories taxonomical focus, geographical focus and spatial extent variables, to characterize the records focus on taxonomical groups and geographic areas (H2.1). The second PCA was performed in order to characterize the modelling approach of the records (H2.2) considering the categories of modelling approach, management type, whether the model was spatially explicitly, and cost evaluation of management actions. PCA analyses were performed in Statistica v13 (StataCorp., 2013).

3. Results

3.1. Dynamic models in invasion ecology

The number of records considering invasive species related key words (see *Table 2*) in ISI WOS was 27429 publications (Step 1; see Fig. 2). Among these, 7248 records had modelling related key words, 2395 dynamic modelling key words, and 1277 management related key words. An overall increase in the number of records published with invasive species keywords was observed (with the highest increase after 1990), regardless of the potential modelling or management nature (Fig. 3). Yet, the emergence of studies using modelling related keywords was mostly observed from the late 1990s onwards.

This trend was also perceived for records dealing with dynamic modelling related key words and management related keywords, thereby confirming hypotheses H1.1 and H1.2. A peak in integration of dynamic models keywords and management keywords within general papers with modelling keywords and with dynamic related keywords, respectively, was observed in the early 1990s. Conversely, the modelling keywords within studies with invasive species related keywords have increased consistently along time (Fig. 3).

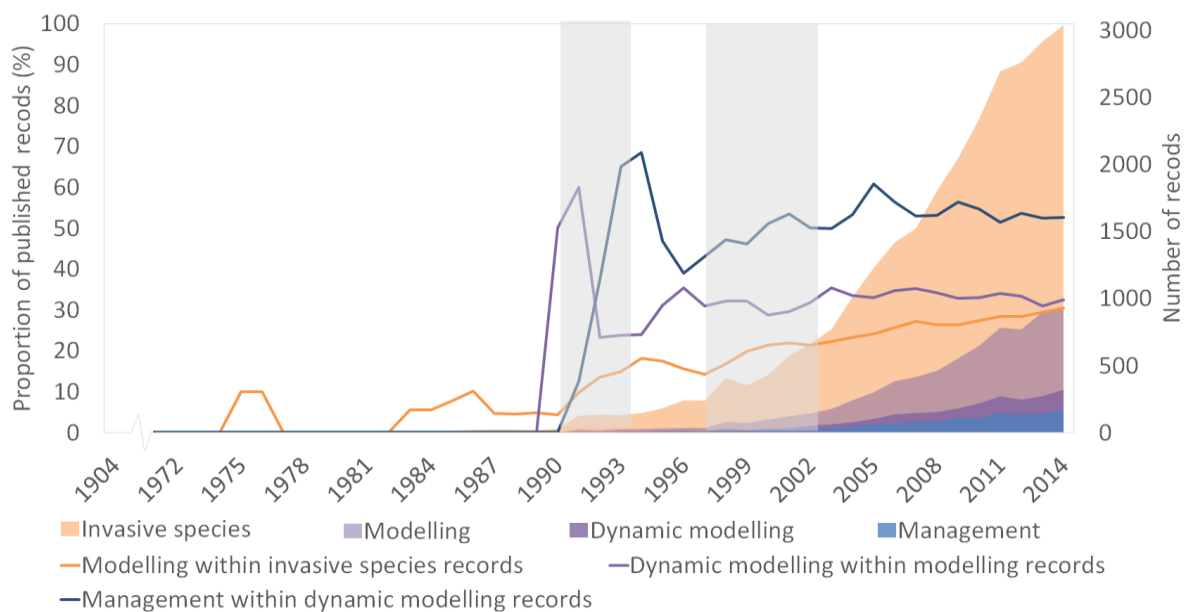


Fig. 3 - The number of records retrieved by the search for literature considering invasive species, modelling, dynamic modelling and management keywords in ISI Web of Science (ISI WOS) from 1904 to 2014 (smoothing curves showing averages for 2-year time periods; on the right y-axis). The figure also illustrates the proportions of modelling inside the invasive species records, of dynamic modelling inside the modelling invasive species records, and of management inside the dynamic modelling of invasive species (on the left y-axis). Important time periods, discussed in more detail (see section 3.1) are highlighted with a light grey shadowing. Gaps in the x-axis represent the time intervals for which no significant number of records were retrieved by our search.

3.2. Taxonomic and geographic focus

From the total set of records considered in the literature search (Fig. 2; $n = 1849$), 20% (corresponding to 369 records) were considered suitable for literature review (see Supplementary Table 1). The earliest record focused on modelling for biological invasion management purposes was found for year 1997, regarding the invasive plant *Acacia saligna* (Higgins et al., 1997). In 1998, several invertebrates and vertebrates were targeted for the first time in published management models. Examples were *Lymantria dispar* (gypsy moth; Sharov and Liebhold, 1998, Sharov et al., 1998), *Dreissena polymorpha* (zebra mussel; Schneider et al., 1998) and the toad *Bufo marinus* (Lampo and De Leo, 1998). Other taxa were only mentioned in 2005, with emphasis on phytoplankton modelling (Petrovskii et al., 2005).

Altogether, plants were the most represented taxonomic groups (44.27%), followed by invertebrates (32.80%) and then by vertebrates (18.15%). The other taxa represented only the remaining 4.78% records (Fig. 4a). Plants and invertebrates are well represented throughout almost all the years under analysis. The vertebrates although also represented from the beginning show an increase on focus later on, similarly, on a less extent, to other taxonomical groups. The geographical focus of the set of records was generally spread worldwide, with studies being conducted in different parts of the world (Fig. 4b). Still, North America was, by far, the most represented continent (46.57%), followed by Europe (19.86%) and by Oceania (19.49%), and finally by the other continents (11.19%). The studies involving multiple continents were almost residual (2.89%). The earliest study found in our search was conducted in South Africa (in 1997; Higgins et al., 1997), North America and Oceania were first mentioned in 1998 (e.g. Edwards et al., 1998, Lampo and De Leo, 1998), and Europe in 2000 (Wadsworth et al., 2000). The first study focusing in more than one continent was published in 2004 (Morrison et al., 2004). In fact, since 2004, more continents were simultaneously targeted by modelling studies per year (Fig. 4b). The spatial extent was clearly dominated by local studies (86.55%), with regional (12.73%) and global (0.73%) studies representing a smaller fraction (Fig. 4c). The results are mostly in line with the hypothesis proposed (H2.1).

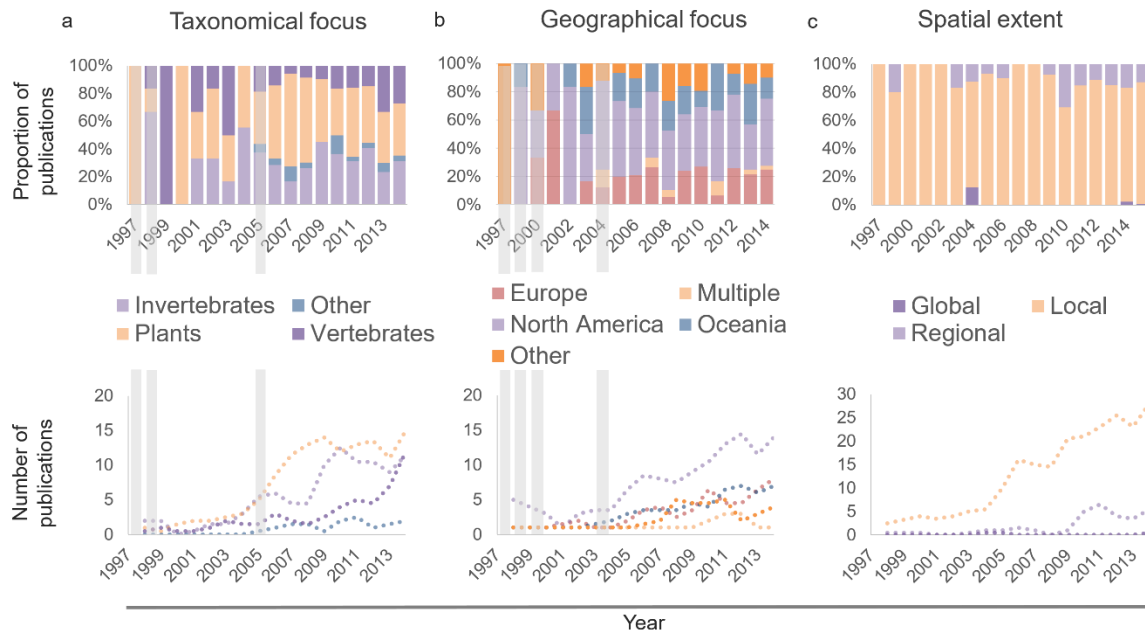


Fig. 4 - Temporal trends by variable analysed in Hypothesis 2.1:(a) Taxonomic focus, (b) Geographical Focus, and (c) Spatial extent. The upper row represents the proportion of publications per year, and the lower row represents absolute number of publications per year (smoothing curves showing averages for 2-year time periods). Time periods discussed in more detail (see section 3.2) are highlighted with a light grey shadowing.

3.3. Characteristics of the modelling approach

The majority of the records considered in the literature search corresponded to studies based on dynamic models (79.78%), being the remaining ones (20.22%) focused on hybrid models (i.e. combined static and dynamic approaches). The first publication on dynamic modelling was found in 1987, and corresponded to a paper on population biology of invaders (Crawley, 1987). Dynamic modelling studies dominated until the beginning of the 2000s. Since 2003, however, hybrid models began to be more frequently used (Fig. 5a). Records including non-spatially explicit models (57.68%) outnumbered those that did include a spatial component (42.31%), though both non-spatially and, later on, spatially explicit modelling increased over the last years (Fig. 5b).

Regarding the type of management applied to the invasive species, both post-establishment actions (active management) and preventive actions (passive management) seemed to increase through time, with an overall predominance of records targeting active management (57.04%; Fig. 5c). Similar trends were observed regarding cost evaluation, with both cost and non-cost evaluations showing increasing values and a similar trend through time (Fig. 5d).

However, only 27.76% of records presented an assessment of management costs. In general, the results are in line with the hypothesis proposed (H2.2).

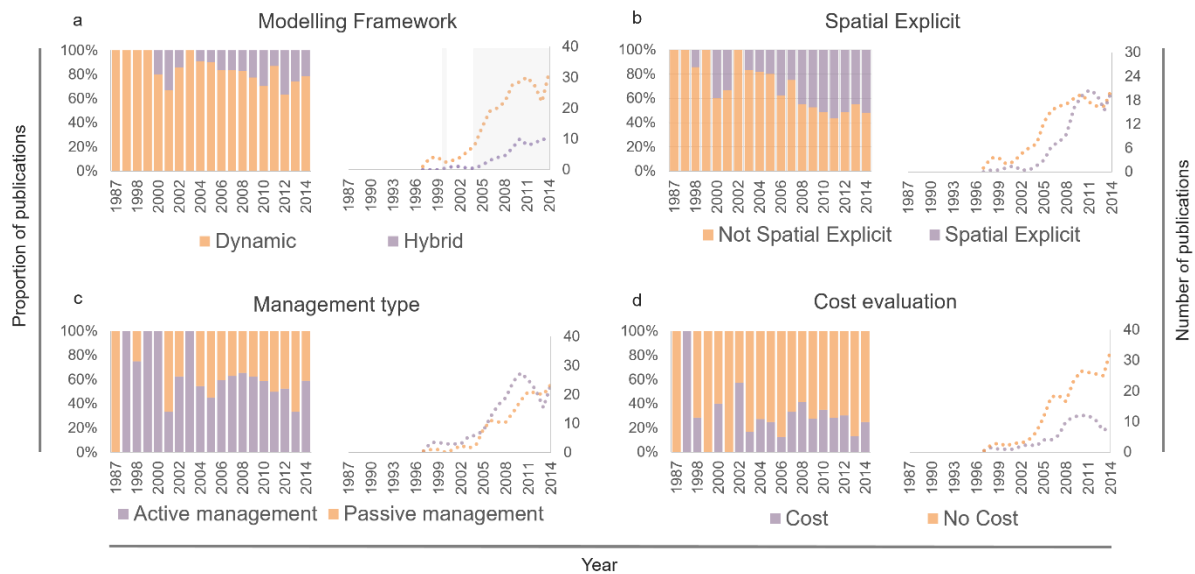


Fig. 5 - Temporal trends by variable analysed in Hypothesis 2.2:(a) Modelling framework, (b) Model spatial explicitly, (c) Management type and (d) Cost evaluation. In each case, the right plots represent the absolute number of publications per year (smoothing curves showing averages for 2-year time periods) and the left plots represent the proportion of publications per year. Time periods discussed in more detail (see section 3.3) are highlighted with a light grey shadowing.

3.4. Modelling publications and invasive species management

The combination of PCA axis 1 and 2 allowed to capture respectively around 45% and 68% of the variation in reviewed records (Fig. 6). The first PCA (Fig. 6a) was conducted considering taxonomical focus, geographical focus and spatial extent, and showed the segregation of two main groups in the ordination space. The first group included the continent “North America”, “Local” extent, and “Plant” taxonomical focus. The second group included also a main subgroup, dominated by the combination of “Vertebrates” with “Regional” spatial extent. The second PCA (Fig. 6b), which incorporated the records classified according to type of modelling framework, model spatial explicitly, type of management and cost evaluation, highlighted two main groups of model attributes along the first axis (Fig. 6b). The first group relates “Passive Management”, “Non cost” evaluation, “Spatial Explicit” and hybrid (“Static-Dynamic”) models. Contrastingly, the second group relates “Active Management”, “Cost” evaluation, “Not Spatial Explicit” and purely “Dynamic” models.

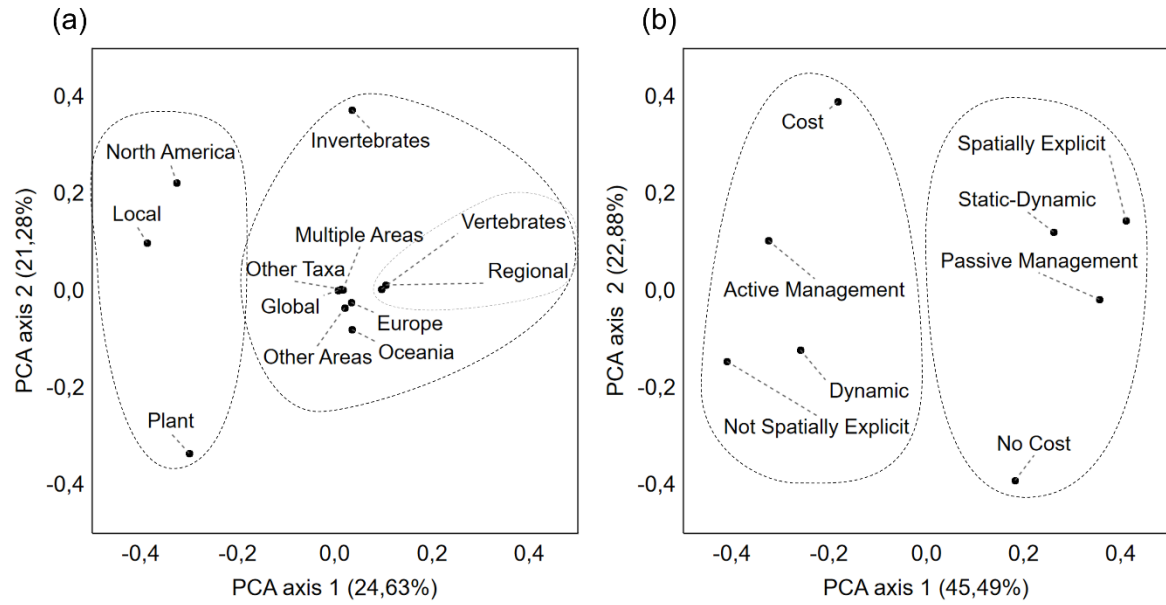


Fig. 6 - Results from principal components analyses (PCA) considering: Taxonomic focus, Geographical focus and Spatial extent (a); and Cost evaluation, Type of management, Spatially explicit nature, and Modelling framework (b). On grey dashed lines highlight two main groups along the first PCA axis and in light grey a minor group. For visualization purposes, variables were plotted as dots instead of lines in the ordination space.

4. Discussion

4.1. The Past: an historical perspective of published invasion research

Biological invasions are a fairly recent topic in science, being established as a discipline since the middle of the XX century, following the publication of *The Ecology of Invasions by Animals and Plants*, by Charles Elton (1958) (Richardson and Pysek, 2008, Simberloff, 2010). The results from our review highlight the rise in number of publication studies on invasive species over the last three decades (cf. Fig. 3). We note, however, that this number rely on the assumption that keywords directly translate into the subject of studies (from now on this assumption underlies our analyses and discussions). The proliferation of publications on biological invasions since the early 1990s and its popularization has been already reported by several studies (Davis, 2006, Lockwood et al., 2013, Ricciardi and MacIsaac, 2008, MacIsaac et al., 2010, Simberloff, 2010, Lowry et al., 2012). This expansion has been associated with the 1982 SCOPE program (Davis, 2006, Simberloff, 2010), since which biological invasions became a key issue to academics and stakeholders focused on the conservation, environmental, and social-economic implications of invasions (McNeely, 2001, Hobbs and Richardson, 2010, Humair et al., 2015). Moreover, this rising concern resulted in a growing availability of invasion data, allowing for more accurate quantitative analysis and for modelling predictions to become a hallmark on the field of invasions (Ricciardi and MacIsaac, 2008, Simberloff, 2010).

The application of modelling techniques on invasive species can be traced back to the beginning of the XX century with Cooks' works on predicting habitat suitability (e.g. Cook, 1924, see Sutherst, 2014). The application of dynamic modelling may further go back to the middle of the XX century, with the work on "*Random dispersal in theoretical populations*" by Skellam (1951). Our bibliographic analysis showed that studies focusing on the (dynamic) modelling of invasive species only started to become frequent since the late 1990s (Fig. 3). The expansion of modelling studies in the late 1990s matches results from other assessments focused on modelling literature (Jørgensen, 2008). In fact, Jørgensen (2008) showed that the number of modelling articles published from 2001 to 2006 was about nine times the number of papers published from 1975 to 1980. From the mid-1990s, the comprehensive use of ecological models has showed a constant and remarkable growth among publications on biological invasions. This may be attributed to developments in computer technology and to advances in the general knowledge about invasion phenomena with the accumulation of relevant data bases (Davis, 2006, Jørgensen and Fath, 2011, Simberloff, 2010).

Based on our results, dynamic models represented roughly one third of the modelling publications focused on invasive species (see Fig. 3). From these, about one half of the approaches were designed for management purposes. Compared with dynamic modelling techniques, applied to biological invasions from the beginning, static approaches have a more recent prevalence in the field of invasions (Jørgensen, 2008). According to Jørgensen (2008), from 1975 to 1980, studies with dynamic models represented more than 90% of the publications in ecological modelling. From 2001 to 2006, dynamics modelling studies still comprised more than half of the modelling publications, with new approaches growing such as static biogeochemical and bioenergetics models, individual based models, cellular automata models and spatially explicit models. Static approaches should represent no more than 15% of modelling studies from 2001 to 2006 (Jørgensen, 2008).

The large focus on dynamic modelling for the management of invasive species may be attributed to an increasing pressure to tackle invasive species, namely through the European Environment Agency report on invasive species in 1998 (see Davis, 2006). Other key initiatives were the Clinton administration's (1999) directives to prevent and control alien invasive species in the US, the 2000 IUCN "Guidelines for the prevention of biodiversity loss caused by alien invasive species", and the National Research Council 2002 report on the Scientific basis for predicting the invasive potential of nonindigenous plant and plant pests in the United states (see Davis, 2006). Shigesada and Kawasaki (1997) book on "*Biological invasions: theory and practice*" may be symptomatic of the increasing focus of dynamic modelling on invasive species management in the late 1990s (Davis, 2006). Shigesada and Kawasaki (1997) reviewed mathematical modelling applications in invasion ecology, resulting from the appeal for a higher need to understand and predict invasive species.

The growing need to tackle invasive species and the many institutional incentives to do so have fostered further application of dynamic modelling approaches in the management of invasions. The Millennium Ecosystem Assessment (MA, 2005) highlighted the threats posed by invasive species on biodiversity, ecosystem services and human well-being across biomes. The World Organization for Animal Health (OIE) and the International Plant Protection Convention (IPPC) both stressed management priorities for alien species (Keller et al., 2011), among other institutions and initiatives (see Shine et al., 2010, for a review on former UE policy to combat invasive species). Throughout this process of growing awareness and knowledge production, the need to incorporate dynamic modelling approaches to support the decision-making for invasion management has been repeatedly emphasized (Hulme, 2006, Gallien et al., 2010, Cuddington et al., 2013).

4.2. The Present: current trends in the modelling of biological invasions

Invasive species are spread across taxonomic groups and occur in most regions of the world (Pysek et al., 2008). Our literature review allowed identifying the taxonomical and geographical tendencies of research on the application of dynamic modelling for invasive species management. In general, a large portion of the studies was focused on plants and invertebrates, and was performed in developed regions (Fig. 5). This is consistent with previous studies that showed a biased focus on invasion ecology and more broadly in ecology (Martin et al., 2012, Kueffer et al., 2013, Ruiz et al., 2000, Wilson et al., 2007, Dana et al., 2014, Pysek et al., 2008). Almost a decade ago, Pysek et al. (2008) already observed that plants and insects were the most represented groups in invasive species studies, together accounting for almost two-thirds of the taxa studied, and that almost half of all invasive species, and more than half of the studies conducted, were related to North America. In parallel, Martin et al. (2012) revealed that countries with the highest Gross National Income (GNI) were overrepresented in their analyses of the global distribution and environmental context of terrestrial field studies, published in 10 highly cited ecology journals over a 5-year period.

One of the main issues driving the selection of target organisms in invasion research has been the magnitude of the ecological impacts and the level of invasiveness of each species (Pysek et al., 2008). For instance, weeds and pests tended to be more targeted by invasion studies, mostly due to their economic impacts in agriculture and forestry sectors (Wilson et al., 2007). On the other hand, a bias in the target geographic areas could be associated with research intensity inequality, since the focus on research is mostly conditioned by economic priorities and practical limitations than by geographical and socio-political barriers (Wilson et al., 2007, Pysek et al., 2008). The economy of a given region can affect directly and/or indirectly the research efforts and, historically, the system of science and education that are better developed allow for greater research intensity (Pysek et al., 2008). Our review may have failed to capture the whole geographic pattern of invasion research since our search was conducted solely based on English keywords.

From our results, a relation was observed between “North America”, “Local” extent, and “Plant” taxonomical focus (Fig. 6). This could be explained by a long history of weed management in the United States (Timmons, 2005), as exemplified in the studies from Edwards et al. (1998) on *Lythrum salicaria* biological control, Rinella and Sheley (2005) model for predicting invasive weed and grass dynamics or Shyu et al. (2013) density-dependent seasonal model for the

management of an invasive weed, the garlic mustard (*Alliaria petiolata*). Also we found a smaller relation between “vertebrates” taxonomical focus and “regional” extents, which may be explain by the higher mobility of some vertebrate species, occupation of larger habitats and/or the availability of large-scale datasets.

An increased demand to understand, analyse, and forecast invasion processes has fostered the use of models and specifically of dynamic models in invasion studies (Gallien et al., 2010). Yet, dynamic modelling still represents a small proportion of the modelling applications in invasion research (see Fig. 3), probably because of the data requirements and the more complex model structures for which better expert knowledge and reductionist parameterization is required. From our analyses, the combination of static and dynamic modelling approaches (i.e. hybrid models) has been growing (see Fig. 4) and may pave the way to modelling species distributions on the basis of large-scale relationships, while at the same time considering the most important dynamic processes (Gallien et al., 2010).

In fact, hybrid models, specifically static-dynamic combinations, have been increasing, a trend that seems to be related with passive management options and spatially explicit models and, in a lesser extent, with no evaluation of management costs (see Fig. 5). Combining static models and dynamic models is expected to allow spatial explicit modelling, as opposed to dynamic models that may not be spatially explicit (e.g. Classical population models, Chen et al., 2011). The importance of static approaches, such as habitat suitability models, that are particularly effective in predicting invasions in a spatially explicit environment, may justify the relation between hybrid model approaches and passive management options, since predicting invasions is of primary importance for preventive invasion management (e.g. Vicente et al., 2016). The association to no cost evaluation may relate to the fact that passive management options may not rely on a budget (see Dana et al., 2014 for similar results), in opposition to active management that entails costs.

Active management options also showed a relation to purely dynamic modelling options and to models that are not spatially explicit (see Fig. 5). The ability of dynamic models to better mimic demographic processes, such as dispersal (Hastings et al., 2005) and growth (Jongejans et al., 2008), is of key importance for control measures, and this may explain the relation of active management to dynamic modelling. On the other hand, the relation between dynamic and non-spatial models may be due to the difficulty to spatialize purely dynamic models. Nevertheless, new platforms combining different approaches to investigate the large-scale holistic relationships (“top-down”), while at the same time considering the most important processes (“bottom-up”) (e.g. Bastos et al., 2012, Santos et al., 2013, Soares-Filho et al.,

2009), will potential pave the way for spatially-explicit dynamic modelling in invasion biology (Santos et al., 2015).

4.3. The Future: further enhancing invasion modelling and management

Invasion biology has for long been a discipline focused on understanding invasion processes, for example what makes an invasion thrive (invasiveness) or what makes a habitat prone to invasion (invasibility). But an urge for a transition to a more practical discipline, that is able to work with and for stakeholders, and to provide solutions, has been placed (Hulme, 2003, Hobbs and Richardson, 2010). The importance of effectively tackling invasions leads to the need to devise and implement management actions, and likewise to work with managers and inform them on optimal management options. To do so, predictive modelling has the ability to mimic invasion processes and predict invasions, allowing transparent assumptions and the ability to extrapolate beyond known conditions, including multiple management scenarios (Cuddington et al., 2013).

Our review has showed that the application of dynamic modelling in the management of invasive species has been evolving in recent years. This has probably been due to technical improvements, to the increased availability of data and knowledge on invasive species, and ultimately to the increased appraisal of this type of modelling approaches due to their ability to model global change phenomena (Gallien et al., 2010). Hybrid static-dynamic models may well be a future stepping stone towards the spatialization of model simulations and management options but this could later be a dropped approach to more sophisticated dynamic modelling approaches that will allow to fully and easily implement ecological based models (Bastos et al., 2012). Likewise, the need to incorporate socio-economic dimensions to better optimize management strategies, describing cost and effectiveness of management strategies (Cuddington et al., 2013), will further empower dynamic approaches.

A broader consideration of invasive species impacts when prioritizing and developing models will also contribute to improve their usefulness for management. From these impact-driven models, efficient monitoring and management strategies can be designed to restore ecosystems functions and communities that have been damaged by biological invasions (Vicente et al., 2016). A strong emphasis should be given to those dynamic modelling approaches that simultaneously attempt to capture the structure and the composition in systems affected by long-term environmental disturbances (Jørgensen, 1994) induced by

invasion processes. Finally, the strategic role of models and their predictions to effectively communicate conservation and management outcomes to stakeholders (Guisan et al., 2013) should also be emphasized in the scope of adaptive invasion management.

5. Conclusions and Final Remarks

In order to address the proposed major goals, the following main conclusions may be highlighted from our review study on the application of dynamic models to support invasion research and management.

Considering the first goal, *to examine the extent to which dynamic modelling has been used to address biological invasions worldwide*, ecological modelling, and specifically dynamic modelling, has been increasingly used in the scope of invasion biology, both to support research and management. In fact, the observed trends may be associated to 1982 SCOPE program which brought attention to the implications of invasion sparking a growing awareness and focus from academics and stakeholders. This attention resulted in an accumulation of available invasion data, allowing for more accurate quantitative analysis and for modelling predictions. Adding a growing institutional pressure to tackle invasive species, such factors may have contributed to an increased application of ecological modelling approaches to better understand, predict, and forecast invasive species distributions.

Regarding the second goal, *to understand how dynamic modelling approaches have evolved with time, regarding management strategies targeting biological invasions* it was possible to conclude that the application of dynamic modelling approaches to manage invasive species has been biased both geographically (e.g. North America and Europe) and taxonomically (e.g. plants and invertebrates). The geographical bias can be related with the level of countries developed, as developed countries usually present a strong and established system of science and education, allowing a continued improvement in the produced scientific knowledge. The taxonomical bias can be related with the interest to target invasive species causing the highest ecological and/or economic impacts (e.g. weeds and insect pests).

As to the understanding on how this technic has been applied regarding management strategies, dynamic modelling has had a particularly important application in the design and evaluation of management actions, mainly at more local scales. The ability of dynamic models to capture underlying invasion processes as invasive species demography, for example, is of key importance to support planning and to implement control actions. On the other hand, the combination of static and dynamic models have showed to be have an increasing role on supporting preventive management strategies.

It can therefore be concluded that static and dynamic models act as complementary approaches allowing on one hand take into account large-scale patterns, while on the other hand consider the most important fine-scale dynamic processes underlying biological

invasions. Such combination of dynamic and static models may be particularly relevant to support invasion management, and further methodological developments should be considered a research priority.

From this study, we can highlight that:

- ❖ Ecological modelling has been increasingly used in invasion biology studies;
- ❖ Dynamic modelling in invasion management had biased applications concerning geographical and taxonomical focus.
- ❖ Dynamic modelling has been largely useful for local management of invasive species;
- ❖ Static-dynamic hybrid models have showed to be useful complementary approaches;
- ❖ Hybrid models have found to be the most relevant to support preventive stages of invasion management;
- ❖ Hybrid models must represent a priority for future invasion research and prioritization of management efforts.

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Title page images references:

Left image (*Dreissena polymorpha*): mexilhao zebra, n.d. photograph, viewed 5 July 2016, <<http://www.netxplica.com/images/animais/mexilhao.zebra.2.jpg>>.

Central image (*Acacia saligna*): acacia, n.d. photograph, viewed 5 July 2016, <http://invasoras.pt/wp-content/uploads/2012/12/acacia_saligna-95small16por9-800x399.jpg>.

Right image (*Lymantria dispar*): entomart, 2006, Lymantria dispar01, photograph, viewed 5 July 2016 <https://upload.wikimedia.org/wikipedia/commons/f/f3/Lymantria_dispar01.jpg>.

Appendix

Supplementary Table 1- Literature review of records regarded as suitable for revision. Literature review and classification according to the seven categories, Modelling framework, Cost evaluation, Management option (active - A, passive - P), Geographical option, Spatial extent, Model spatially explicitly and taxonomical focus. (see Table 4 for full Hypotheses, categories/associated questions, and classification).

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Frésard and Ropars-Collet, 2014)	2014	Invertebrates	Europe	Local	Not combined with a species static model	No	A	Yes
(Büyüktaktakin et al., 2011)	2011	Plants	North America	Local	Not combined with a species static model	Yes	A	Yes
(Nehrbass et al., 2006)	2006	Plants	Europe	Local	Not combined with a species static model	Yes	P	No
(Marten and Moore, 2011)	2011	Invertebrates	North America	Local	Not combined with a species static model	No	A,	Yes
(Sebert-Cuvillier et al., 2007)	2007	Plants	Europe	Local	Not combined with a species static model	No	A	No
(Hyytiäinen et al., 2013)	2013	Invertebrates	Europe	Local	Not combined with a species static model	No	P	Yes
(Ceddia et al., 2009)	2009	Invertebrates	Europe	Regional	Not combined with a species static model	No	A	Yes
(Grechi et al., 2014)	2014	Plants	Oceania	Local	Not combined with a species static model	No	A	No
(Colomer et al., 2014)	2014	Invertebrates	Europe	Local	Not combined with a species static model	Yes	A, P	No
(Tonini et al., 2014)	2014	Invertebrates	North America	Local	Not combined with a species static model	Yes	P	No
(Büyüktaktakin et al., 2014)	2014	Plants	North America	Local	Not combined with a species static model	Yes	A	Yes
(Mammeri et al., 2014)	2014	Other taxa	No reference	Local	Not combined with a species static model	Yes	A	No
(Epanchin-Niell et al., 2014)	2014	Invertebrates	Oceania	Regional	Combined with a species static model	Yes	A, P	No
(Meier et al., 2014)	2014	Plants	Europe	Local	Combined with a species static model	Yes	A	Yes
(Teem et al., 2014)	2014	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(Teem and Gutierrez, 2014)	2014	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(Wang et al., 2014)	2014	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(Yang et al., 2014)	2014	Not specified	No reference	no reference	Not combined with a species static model	Yes	A	No
(Ferrari et al., 2014)	2014	Invertebrates	North America	Local	Not combined with a species static model	Yes	P	No
(Savage and Renton, 2014)	2014	Invertebrates, Other taxa	No reference	Local	Not combined with a species static model	Yes	A, P	No
(Potts et al., 2014)	2014	Vertebrates	Oceania	Regional	Combined with a species static model	Yes	A, P	No
(Bueyuektahtakin et al., 2014)	2014	Plants	North America	Local	Not combined with a species static model	Yes	A	Yes
(Kovacs et al., 2014)	2014	Invertebrates	North America	Local	Not combined with a species static model	Yes	A	Yes
(Labonne et al., 2013)	2013	Vertebrates	Other	Local	Not combined with a species static model	Yes	P	No

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Gutierrez and Ponti, 2013a)	2013	Invertebrates	North America	Regional	Combined with a species static model	No	A	Yes
(Tonini et al., 2013)	2013	Invertebrates	North America	Local	Not combined with a species static model	Yes	P	No
(Lu et al., 2013)	2013	Plants	Other	Local	Combined with a species static model	Yes	P	No
(Richter et al., 2013)	2013	Plants	Europe	Regional	Combined with a species static model	Yes	A, P	Yes
(Forsyth et al., 2013)	2013	Vertebrates	Oceania	Local	Combined with a species static model	Yes	P	No
(Malchow et al., 2013)	2013	Plants	No reference	Local	Not combined with a species static model	Yes	A	No
(Bertolucci et al., 2013)	2013	Plants	No reference	no reference	Not combined with a species static model	No	A	Yes
(Brown et al., 2012)	2012	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Chivers and Leung, 2012)	2012	Not specified	North America	Local	Not combined with a species static model	No	P	No
(Moore and Runge, 2012)	2012	Plants	Oceania	Local	Not combined with a species static model	No	A	Yes
(Iordan et al., 2012)	2012	Vertebrates	Europe	Regional	Combined with a species static model	Yes	A, P	No
(Gutierrez et al., 2012a)	2012	Invertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Evans et al., 2012)	2012	Plants	North America	Local	Combined with a species static model	No	A	No
(Sutrave et al., 2012)	2012	Other taxa	North America	Regional	Not combined with a species static model	Yes	P, P	Yes
(Gallardo et al., 2012)	2012	Invertebrates	Europe	Local	Combined with a species static model	Yes	P	No
(Wang et al., 2012)	2012	Plants	North America	Local	Not combined with a species static model	Yes	A	Yes
(Fitzpatrick et al., 2012)	2012	Invertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Epanchin-Niell and Wilen, 2012)	2012	Not specified	No reference	no reference	Not combined with a species static model	Yes	A	Yes
(Pichancourt et al., 2012)	2012	Plants	Oceania	Local	Not combined with a species static model	No	A	Yes
(Guichard et al., 2012)	2012	Invertebrates	Oceania	Local	Not combined with a species static model	Yes	P	No
(Emry et al., 2011)	2011	Plants	North America	Local	Not combined with a species static model	Yes	A, P	No
(Gertzen and Leung, 2011)	2011	Invertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Stanaway et al., 2011b)	2011	Invertebrates	Oceania	Local	Not combined with a species static model	Yes	P	No
(Travis et al., 2011)	2011	Plants	Europe	Local	Not combined with a species static model	Yes	A, P	No
(Liu et al., 2011)	2011	Not specified	Oceania	Local, Regional	Not combined with a species static model	No	P	Yes
(Kotani et al., 2011)	2011	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Stanaway et al., 2011a)	2011	Not specified	Oceania	Local	Not combined with a species static model	Yes	A, P	No
(Moore et al., 2011)	2011	Invertebrates	North America	Local	Not combined with a species static model	No	A	Yes
(Pitt et al., 2011)	2011	Plants	Oceania	Regional	Combined with a species static model	Yes	P	No

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Wang et al., 2011)	2011	Plants	North America	Local	Combined with a species static model	Yes	P	No
(Baxter and Possingham, 2011)	2011	Invertebrates	Oceania	Local	Combined with a species static model	Yes	P	Yes
(Cacho and Hester, 2011)	2011	Not specified	No reference	no reference	Not combined with a species static model	Yes	A, P	Yes
(Krug et al., 2010)	2010	Plants	Other	Local	Not combined with a species static model	Yes	A	Yes
(Albers et al., 2010)	2010	Not specified	No reference	no reference	Not combined with a species static model	Yes	A	Yes
(Haight and Polasky, 2010)	2010	Not specified	No reference	no reference	Not combined with a species static model	No	A, P	Yes
(Kaiser and Burnett, 2010)	2010	Vertebrates	North America	Local	Not combined with a species static model	Yes	A, P	Yes
(Økland et al., 2010)	2010	Other taxa	Europe	Regional	Not combined with a species static model	No	A	No
(Carrasco et al., 2010b)	2010	Invertebrates	Europe	Regional	Combined with a species static model	Yes	A, P	No
(Olson and Roy, 2010)	2010	Not specified	No reference	no reference	Not combined with a species static model	No	A, P	Yes
(Kotani et al., 2010)	2010	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Wu et al., 2010)	2010	Invertebrates	North America	Local	Combined with a species static model	No	P	No
(Chizinski et al., 2010)	2010	Vertebrates	North America	Local	Not combined with a species static model	No	A	No
(Wesseler and Fall, 2010)	2010	Invertebrates	Europe	Regional	Not combined with a species static model	Yes	A, P	Yes
(Kadoya and Washitani, 2010)	2010	Invertebrates	Other	Local	Combined with a species static model	Yes	A, P	No
(Smolik et al., 2010)	2010	Plants	Europe	Regional	Combined with a species static model	Yes	P	No
(Prasad et al., 2010)	2010	Invertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Kim et al., 2010)	2010	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Blackwood et al., 2010)	2010	Plants	North America	Local	Not combined with a species static model	Yes	A	Yes
(de-Camino-Beck and Lewis, 2009)	2009	Plants	North America	Local	Not combined with a species static model	Yes	A	No
(Mari et al., 2009)	2009	Invertebrates	Europe	Local	Not combined with a species static model	Yes	P	No
(Robinet and Liebhold, 2009)	2009	Invertebrates	North America	Local	Not combined with a species static model	Yes	A, P	No
(Frid and Wilmschurst, 2009)	2009	Plants	North America	Local	Not combined with a species static model	Yes	A	No
(Harris et al., 2009)	2009	Plants	Europe	Local	Not combined with a species static model	Yes	A	No
(Estay et al., 2009)	2009	Invertebrates	Other	Local	Not combined with a species static model	Yes	P	No
(Jiao et al., 2009)	2009	Vertebrates	Other	no reference	Combined with a species static model	No	P	No
(Fox et al., 2009)	2009	Plants	Oceania	Local	Not combined with a species static model	Yes	A, P	No
(Pitt et al., 2009)	2009	Invertebrates	Oceania	Local	Combined with a species static model	Yes	P	No
(Kotani et al., 2009b)	2009	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Yamanaka and Liebhold, 2009)	2009	Invertebrates	No reference	no reference	Not combined with a species static model	No	A	No

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Boukal and Berec, 2009)	2009	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Ferrari and Lookingbill, 2009)	2009	Not specified	North America	Local	Combined with a species static model	Yes	A	No
(Yemshanov et al., 2009)	2009	Invertebrates	North America	Regional	Not combined with a species static model	Yes	P	No
(Potapov, 2009)	2009	Invertebrates	No reference	Local	Not combined with a species static model	No	A	Yes
(Yokomizo et al., 2009)	2009	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Hester and Cacho, 2009)	2009	Invertebrates	No reference	Local	Not combined with a species static model	Yes	A, P	Yes
(Hyder et al., 2008)	2008	Plants	North America	Local	Not combined with a species static model	Yes	A	Yes
(Grimsrud et al., 2008)	2008	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Olson and Roy, 2008)	2008	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Murphy et al., 2008)	2008	Plants	Oceania	Local	Not combined with a species static model	No	P	No
(Bogich et al., 2008)	2008	Invertebrates	North America	Local	Not combined with a species static model	No	A, P	Yes
(Firn et al., 2008)	2008	Plants	Oceania	no reference	Not combined with a species static model	No	A	No
(Fitt et al., 2008)	2008	Other taxa	Multiple	Local	Combined with a species static model	Yes	P	Yes
(Guichón and Doncaster, 2008)	2008	Vertebrates	Other	Local	Combined with a species static model	Yes	A, P	No
(Eiswerth and Van Kooten, 2007)	2007	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Rew et al., 2007)	2007	Not specified	No reference	Local	Combined with a species static model	Yes	A, P	Yes
(Drury et al., 2007)	2007	Not specified	No reference	no reference	Not combined with a species static model	Yes	P	No
(De-Camino-Beck and Lewis, 2007)	2007	Plants	Multiple	no reference	Not combined with a species static model	No	A	No
(Mehta et al., 2007)	2007	Invertebrates	No reference	no reference	Not combined with a species static model	No	A, P	Yes
(Ooperi and Jolma, 2007)	2007	Invertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Baxter et al., 2007)	2007	Not specified	No reference	no reference	Combined with a species static model	No	A	Yes
(Tattoni et al., 2006)	2006	Vertebrates	Europe	Regional	Combined with a species static model	Yes	P	No
(Jongejans et al., 2006)	2006	Plants	Europe	Local	Not combined with a species static model	No	A	No
(Regan et al., 2006)	2006	Plants	Oceania	Local	Not combined with a species static model	No	A, P	Yes
(Bar-David et al., 2006)	2006	Other taxa	Other	Local	Not combined with a species static model	Yes	A, P	No
(Pausas et al., 2006)	2006	Plants	Europe	Local	Not combined with a species static model	Yes	A	No
(Deines et al., 2005)	2005	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Koop and Horvitz, 2005)	2005	Plants	North America	Local	Not combined with a species static model	Yes	P	No
(Petrovskii et al., 2005)	2005	Other taxa	No reference	Local	Not combined with a species static model	No	A	No
(Sharov, 2004)	2004	Invertebrates	North America	Local	Not combined with a species static model	No	A	Yes

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Smith et al., 2004)	2004	Invertebrates	Other	Local	Combined with a species static model	Yes	P	No
(Morrison et al., 2004)	2004	Invertebrates	Global	Global	Not combined with a species static model	Yes	P	No
(Buckley et al., 2003)	2003	Plants	Oceania	Local	Not combined with a species static model	Yes	A	No
(Leung et al., 2002)	2002	Invertebrates	North America	Local	Not combined with a species static model	No	A, P	Yes
(Eiswerth and Johnson, 2002)	2002	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Perrings, 2002)	2002	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Lurz et al., 2001)	2001	Vertebrates	Europe	Local	Combined with a species static model	Yes	P	No
(Higgins et al., 2000)	2000	Plants	Other	Local	Not combined with a species static model	Yes	A	Yes
(Schneider et al., 1998)	1998	Invertebrates	North America	Local	Not combined with a species static model	Yes	P	No
(Marchi et al., 2014)	2014	Invertebrates	Europe	Local	Not combined with a species static model	No	P	Yes
(Hamilton et al., 2014)	2014	Plants	Europe	Local	Combined with a species static model	Yes	P	No
(Berec et al., 2014)	2014	Invertebrates	North America	Local	Not combined with a species static model	Yes	A, P	Yes
(Lander et al., 2014)	2014	Invertebrates	Europe	Local	Not combined with a species static model	Yes	P	No
(Fennell et al., 2012)	2012	Plants	Europe	Local	Not combined with a species static model	Yes	P	No
(Adams and Lee, 2012)	2012	Invertebrates	North America	Local	Combined with a species static model	No	A, P	Yes
(Murphy et al., 2012)	2009	Plants	No reference	Local	Not combined with a species static model	Yes	A	No
(Jongejans et al., 2011a)	2011	Plants	No reference	Local	Not combined with a species static model	Yes	P	No
(Gutierrez and Ponti, 2011)	2011	Invertebrates	Multiple	Local, Regional	Not combined with a species static model	Yes	P	No
(Harris et al., 2011)	2011	Plants	Europe	Local	Combined with a species static model	Yes	P	No
(Jayasuriya et al., 2011)	2011	Plants	No reference	Local	Not combined with a species static model	Yes	A, P	Yes
(Anderson et al., 2010)	2010	Invertebrates	Oceania	Regional	Combined with a species static model	Yes	P	No
(Sapoukhina et al., 2010)	2010	Other taxa	No reference	Local	Combined with a species static model	Yes	P	No
(Ooperi and Jolma, 2009)	2009	Invertebrates	Europe	Local	Not combined with a species static model	Yes	A, P	No
(Timar and Phaneuf, 2009)	2009	Invertebrates	North America	Local	Combined with a species static model	Yes	P	Yes
(Luo and Opaluch, 2008)	2008	Invertebrates	North America	Local	Combined with a species static model	Yes	P	Yes
(Chalak-Haghighi et al., 2008)	2008	Plants	Oceania	no reference	Not combined with a species static model	No	A	Yes
(Cristofol and Roques, 2008)	2008	Not specified	No reference	no reference	Not combined with a species static model	Yes	P	No
(Van Mourik et al., 2008)	2008	Plants	Other	Local	Not combined with a species static model	Yes	A	No
(Gutierrez et al., 2008)	2008	Invertebrates	North America	Local	Not combined with a species static model	Yes	A	No

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Dauer et al., 2007)	2007	Plants	North America	Local	Not combined with a species static model	Yes	A	No
(Johnson et al., 2006)	2006	Invertebrates	North America	Local	Combined with a species static model	Yes	A	No
(Cacho, 2006)	2006	Not specified	No reference	Local	Not combined with a species static model	No	A	Yes
(Kim et al., 2006)	2006	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Macpherson et al., 2006)	2006	Plants	No reference	Local	Not combined with a species static model	No	P	No
(Odom et al., 2003)	2003	Plants	Oceania	Local	Not combined with a species static model	No	A	Yes
(Eiswerth and Van Kooten, 2002)	2002	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Wadsworth et al., 2000)	2000	Plants	Europe	Local	Combined with a species static model	Yes	A	No
(Finnoff et al., 2005)	2005	Invertebrates	North America	Local	Not combined with a species static model	No	A	Yes
(Higgins et al., 1997)	1997	Plants	Other	Local	Not combined with a species static model	No	A	Yes
(Shea and Possingham, 2000)	2000	Not specified	No reference	Local	Not combined with a species static model	No	A	Yes
(Taylor and Hastings, 2004)	2004	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Hoyer et al., 2014)	2014	Invertebrates	North America	Local	Not combined with a species static model	Yes	P	No
(Holbrook et al., 2014)	2014	Vertebrates	North America	Local	Not combined with a species static model	No	P	No
(Kanary et al., 2014)	2014	Invertebrates	North America	Local	Not combined with a species static model	No	A	No
(Giddens et al., 2014)	2014	Vertebrates	North America	Local	Not combined with a species static model	No	A	No
(Woehler et al., 2014)	2014	Vertebrates	Oceania	no reference	Not combined with a species static model	No	P	No
(Chambers et al., 2014)	2014	Plants	North America	Local	Not combined with a species static model	No	A	No
(Miller et al., 2014)	2014	Plants	North America	Local	Not combined with a species static model	No	A	No
(Tanentzap et al., 2014)	2014	Plants	Oceania	Local	Not combined with a species static model	No	A	No
(Grarock et al., 2014)	2014	Vertebrates	Oceania	Local	Not combined with a species static model	No	A	No
(Terauds et al., 2014)	2014	Vertebrates	Other	Regional	Combined with a species static model	Yes	A	No
(Weed and Schwarzländer, 2014)	2014	Plants	North America	Local	Not combined with a species static model	No	A	No
(Gordillo, 2014)	2014	Invertebrates	No reference	no reference	Not combined with a species static model	No	A	Yes
(Donaldson et al., 2014)	2014	Plants	Other	Local	Combined with a species static model	Yes	P	No
(Hughes et al., 2014)	2014	Plants	No reference	no reference	Not combined with a species static model	No	A	Yes
(Krug and Richardson, 2014)	2014	Plants	Other	no reference	Not combined with a species static model	No	A	No
(Adams et al., 2014)	2014	Invertebrates	Europe	Local	Not combined with a species static model	Yes	P	No
(Zhou and Xiao, 2014)	2014	Not specified	No reference	no reference	Not combined with a species static model	No	P	No

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Collingridge et al., 2014)	2014	Plants, Invertebrates	Other	Regional	Combined with a species static model	Yes	P	No
(Manoukis and Hoffman, 2014)	2014	Invertebrates	North America	Local	Not combined with a species static model	No	A, P	No
(Caplat et al., 2014)	2014	Plants	No reference	Regional	Not combined with a species static model	Yes	A	No
(Yackulic et al., 2014)	2014	Vertebrates	North America	Local	Combined with a species static model	No	A, P	Yes
(Melero et al., 2014)	2014	Vertebrates	No reference	no reference	Combined with a species static model	Yes	A	Yes
(Storkey et al., 2014)	2014	Plants	Europe	Regional	Not combined with a species static model	Yes	P	No
(Milchunas and Vandever, 2014)	2014	Vertebrates	North America	Local	Not combined with a species static model	No	A, P	Yes
(Shyu et al., 2013)	2013	Plants	North America	Local	Not combined with a species static model	No	A	No
(Gutierrez and Ponti, 2013b)	2013	Invertebrates	Multiple	Regional	Not combined with a species static model	Yes	A	No
(Papadopoulos et al., 2013)	2013	Invertebrates	North America	Local	Not combined with a species static model	Yes	P	No
(Cruz et al., 2013)	2013	Vertebrates	Oceania	Local	Not combined with a species static model	No	P	No
(Keith and Spring, 2013)	2013	Invertebrates	Oceania	Local	Combined with a species static model	Yes	P	No
(Tompkins et al., 2013)	2013	Vertebrates	Oceania	no reference	Not combined with a species static model	No	P	No
(Maines et al., 2013)	2013	Plants	North America	Local	Not combined with a species static model	No	A	No
(Pertoldi et al., 2013)	2013	Vertebrates	Europe	no reference	Not combined with a species static model	No	A, P	No
(Tran et al., 2013)	2013	Invertebrates	Europe	Local	Not combined with a species static model	No	P	No
(Rajakaruna et al., 2013)	2013	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Wäber et al., 2013)	2013	Vertebrates	Europe	Local	Combined with a species static model	Yes	A	No
(Osunkoya et al., 2013)	2013	Plants	Oceania	Local	Not combined with a species static model	No	A	No
(Erwin et al., 2013)	2013	Plants	North America	Local	Not combined with a species static model	No	P	No
(Tingley et al., 2013)	2013	Vertebrates	Oceania	Local	Not combined with a species static model	Yes	A	No
(McArthur et al., 2013)	2013	Other taxa	Oceania	Local	Not combined with a species static model	Yes	P	No
(Fordham et al., 2012)	2012	Vertebrates	Oceania	Local	Combined with a species static model	No	A	No
(Robinet et al., 2012)	2012	Invertebrates	Europe	Regional	Combined with a species static model	Yes	P	No
(Epanchin-Niell et al., 2012)	2012	Invertebrates	North America	Local	Not combined with a species static model	Yes	A, P	Yes
(Miller et al., 2012)	2012	Plants	No reference	no reference	Not combined with a species static model	No	A	No
(Blackwood et al., 2012)	2012	Invertebrates	North America	no reference	Not combined with a species static model	No	A	No
(Berec and Maxin, 2012)	2012	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Buhle et al., 2012)	2012	Plants	North America	Local	Not combined with a species static model	No	A	Yes

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Carrasco et al., 2012)	2012	Invertebrates	Europe	Local	Combined with a species static model	Yes	A, P	Yes
(Gaeta et al., 2012)	2012	Vertebrates	North America	Local	Not combined with a species static model	No	A	Yes
(Rasmussen and Hamilton, 2012)	2012	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Lehtiniemi et al., 2012)	2012	Invertebrates	Europe	Local	Not combined with a species static model	Yes	P	No
(Herrera et al., 2012)	2012	Plants	Other	Local	Not combined with a species static model	No	A, P	No
(Gutierrez et al., 2012b)	2012	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Arias-González et al., 2011)	2011	Vertebrates	North America	Local	Not combined with a species static model	No	A	No
(Chalak et al., 2011)	2011	Plants	Multiple	no reference	Not combined with a species static model	No	A	Yes
(Davis et al., 2011)	2011	Plants	North America	Local	Not combined with a species static model	No	P	No
(Rebaudo et al., 2011)	2011	Invertebrates	Multiple	Local	Not combined with a species static model	Yes	P	No
(Homans and Horie, 2011)	2011	Not specified	No reference	no reference	Not combined with a species static model	No	P	Yes
(Mercader et al., 2011)	2011	Invertebrates	North America	Local	Not combined with a species static model	Yes	P	No
(Mari et al., 2011)	2011	Invertebrates	North America	Local	Not combined with a species static model	Yes	A	No
(Roy et al., 2011)	2011	Plants	North America	Local	Not combined with a species static model	No	A	No
(Bader and Williams, 2011)	2011	Invertebrates	Oceania	Local	Not combined with a species static model	No	A	No
(Vuilleumier et al., 2011)	2011	Not specified	No reference	no reference	Not combined with a species static model	Yes	A	No
(Schooler et al., 2011)	2011	Plants	Oceania	Local	Not combined with a species static model	No	A	No
(Rothlisberger and Lodge, 2011)	2011	Plants	North America	Local	Not combined with a species static model	No	P	Yes
(Weber et al., 2011)	2011	Vertebrates	North America	Local	Not combined with a species static model	No	A	No
(Shackelford et al., 2011)	2011	Plants	Oceania	Local	Not combined with a species static model	Yes	A	No
(Parshad and Gutierrez, 2011)	2011	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(Bled et al., 2011)	2011	Vertebrates	North America	Regional	Not combined with a species static model	Yes	P	No
(Jongejans et al., 2011b)	2011	Plants	Oceania	Regional	Not combined with a species static model	Yes	A, P	No
(Jesse et al., 2011)	2011	Not specified	No reference	no reference	Not combined with a species static model	Yes	A, P	No
(Vélez-Espino et al., 2010)	2010	Vertebrates	North America	Local	Not combined with a species static model	No	A, P	No
(Sahlin et al., 2010)	2010	Invertebrates	Europe	Local	Combined with a species static model	Yes	P	No
(Agusto and Okosun, 2010)	2010	Plants	No reference	no reference	Not combined with a species static model	No	A	Yes
(Schmidt et al., 2010)	2010	Invertebrates	Oceania	Local	Combined with a species static model	Yes	A, P	No
(Ramula and Buckley, 2010)	2010	Plants	Oceania	Local	Not combined with a species static model	No	A	No
(Leung et al., 2010)	2010	Not specified	No reference	no reference	Not combined with a species static model	Yes	P	No

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Andrew and Ustin, 2010)	2010	Plants	North America	Local	Combined with a species static model	Yes	P	No
(Sanchirico et al., 2010)	2010	Not specified	No reference	no reference	Not combined with a species static model	No	A, P	Yes
(Carrasco et al., 2010a)	2010	Invertebrates	Europe	Regional	Not combined with a species static model	No	A	Yes
(Rauschert et al., 2010)	2010	Plants	North America	Local	Not combined with a species static model	Yes	P	No
(Fabiszewski et al., 2010)	2010	Other taxa	North America	Local	Not combined with a species static model	No	A	No
(Oliveira and Hilker, 2010)	2010	Vertebrates	Other	no reference	Not combined with a species static model	No	A	No
(Yemshanov et al., 2010b)	2010	Invertebrates	North America	Regional	Not combined with a species static model	Yes	P	No
(Mecoli et al., 2010)	2010	Invertebrates	Europe	Local	Not combined with a species static model	No	A, P	No
(Ridley and Ellstrand, 2010)	2010	Plants	North America	Local	Combined with a species static model	No	A	No
(Kollmann et al., 2009)	2009	Plants	Europe	Local	Combined with a species static model	Yes	P	No
(Lee, 2009)	2009	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Epanchin-Niell et al., 2009)	2009	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Schreiber and Lloyd-Smith, 2009)	2009	Not specified	No reference	no reference	Not combined with a species static model	Yes	A	No
(Kotani et al., 2009a)	2009	Vertebrates	Other	Local	Not combined with a species static model	No	A	Yes
(Kriticos et al., 2009)	2009	Plants	Oceania	Local	Not combined with a species static model	No	A	No
(Wang et al., 2009)	2009	Invertebrates	North America	no reference	Not combined with a species static model	No	A	No
(Zipkin et al., 2009)	2009	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Roura-Pascual et al., 2009)	2009	Invertebrates	Europe	Local	Combined with a species static model	Yes	P	No
(Bax and Thresher, 2009)	2009	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Hauser and McCarthy, 2009)	2009	Plants	Oceania	Local	Combined with a species static model	Yes	P	Yes
(Takimoto, 2009)	2009	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Russell et al., 2009)	2009	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(Jia et al., 2009)	2009	Plants	No reference	no reference	Not combined with a species static model	No	A	No
(Rout et al., 2009)	2009	Plants	Oceania	Local	Combined with a species static model	No	P	Yes
(Tonngang et al., 2009)	2009	Invertebrates	Other	Local	Not combined with a species static model	No	A	No
(Maxwell et al., 2009)	2009	Plants	North America	Local	Combined with a species static model	Yes	A, P	Yes
(Brown et al., 2008)	2008	Plants	Other	Local	Combined with a species static model	Yes	P	No
(Ranjan et al., 2008)	2008	Not specified	No reference	no reference	Not combined with a species static model	No	A, P	Yes
(D'Evelyn et al., 2008)	2008	Vertebrates	North America	no reference	Not combined with a species static model	No	A	Yes
(Dunstan and Bax, 2008)	2008	Invertebrates	Oceania	Local	Not combined with a species static model	Yes	A	Yes

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(McMahon and Metcalf, 2008)	2008	Plants	No reference	no reference	Not combined with a species static model	No	A	No
(Ramula et al., 2008)	2008	Plants	No reference	no reference	Not combined with a species static model	No	A	No
(Sebert-Cuvillier et al., 2008)	2008	Plants	Europe	Local	Combined with a species static model	Yes	P	No
(Potapov and Lewis, 2008)	2008	Invertebrates	No reference	Local	Not combined with a species static model	No	A	Yes
(Le Maitre et al., 2008)	2008	Plants	Other	Local	Not combined with a species static model	Yes	A	No
(Lee et al., 2008)	2008	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Huang et al., 2008)	2008	Plants	Other	Local	Not combined with a species static model	Yes	P	No
(Drury and Rothlisberger, 2008)	2008	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Lye et al., 2007)	2008	Invertebrates	North America	Local	Not combined with a species static model	No	A	No
(Hall and Hastings, 2007)	2007	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Cacho et al., 2007)	2007	Plants	No reference	no reference	Not combined with a species static model	No	A, P	Yes
(Morozov et al., 2007)	2007	Other taxa	No reference	no reference	Not combined with a species static model	No	A	No
(Raghu et al., 2007)	2007	Plants	Oceania	no reference	Not combined with a species static model	No	A	No
(Thornby et al., 2007)	2007	Plants	North America	Local	Not combined with a species static model	No	A	No
(Kern et al., 2007)	2007	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Gonzales and Gergel, 2007)	2007	Vertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Cook et al., 2007)	2007	Invertebrates	Oceania	no reference	Not combined with a species static model	No	P	Yes
(Buckley et al., 2007)	2007	Plants	Oceania	no reference	Not combined with a species static model	No	A	No
(Boukal et al., 2007)	2007	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Jerde and Lewis, 2007)	2007	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Schutzenhofer and Knight, 2007)	2007	Plants	North America	Local	Not combined with a species static model	No	A	No
(Ferreira et al., 2006)	2006	Invertebrates	Other	Local	Not combined with a species static model	Yes	A, P	No
(Inglis et al., 2006)	2006	Invertebrates	Oceania	Local	Combined with a species static model	Yes	P	No
(Sherfy et al., 2006)	2006	Vertebrates	North America	Local	Not combined with a species static model	No	A	No
(Gutierrez and Teem, 2006)	2006	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(DeWalt, 2006)	2006	Plants	North America	Local	Not combined with a species static model	No	A	No
(Drake et al., 2006)	2006	Invertebrates	North America	Regional	Not combined with a species static model	No	P	No
(Drake and Lodge, 2006)	2006	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Perry and Galatowitsch, 2006)	2006	Plants	North America	Local	Not combined with a species static model	No	A	No
(Hein et al., 2006)	2006	Invertebrates	North America	Local	Not combined with a species static model	No	A	No

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Meurk and Hall, 2006)	2006	Plants	Oceania	Local	Not combined with a species static model	No	A	No
(Govindarajulu et al., 2005)	2005	Vertebrates	North America	Local	Not combined with a species static model	No	A	No
(Mullerova et al., 2005)	2005	Plants	Europe	Local	Not combined with a species static model	No	P	No
(Gilbert et al., 2005)	2005	Invertebrates	Europe	Local	Not combined with a species static model	Yes	P	No
(Hilker et al., 2005)	2005	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Floerl et al., 2005)	2005	Not specified	Oceania	Local	Not combined with a species static model	No	P	No
(Takahashi et al., 2005)	2005	Invertebrates	Other	no reference	Not combined with a species static model	No	A	No
(Sutherst and Maywald, 2005)	2005	Invertebrates	Oceania	Regional	Combined with a species static model	Yes	P	No
(Buhle et al., 2005)	2005	Invertebrates	No reference	no reference	Not combined with a species static model	No	A	Yes
(Emery and Gross, 2005)	2005	Plants	North America	Local	Not combined with a species static model	No	A	No
(Drake, 2005a)	2005	Vertebrates	Europe	Local	Not combined with a species static model	No	P	No
(Bobeldyk et al., 2005)	2005	Invertebrates	North America	Local	Not combined with a species static model	No	P	No
(Merrin et al., 2005)	2005	Plants	Oceania	Local	Combined with a species static model	Yes	P	No
(Travis and Park, 2004)	2004	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes
(Drake, 2004)	2004	Invertebrates	No reference	no reference	Not combined with a species static model	No	P	No
(Neubert and Parker, 2004)	2004	Plants	North America	Local	Not combined with a species static model	No	P	No
(Bartell and Nair, 2004)	2004	Invertebrates	North America	Regional	Not combined with a species static model	No	P	No
(Marvier et al., 2004)	2004	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Watola et al., 2003)	2003	Vertebrates	Europe	Local	Not combined with a species static model	No	A	No
(Doubledee et al., 2003)	2003	Vertebrates	North America	Local	Not combined with a species static model	No	A	No
(Liebhold and Bascompte, 2003)	2003	Invertebrates	North America	Local	Not combined with a species static model	No	A	No
(Havel et al., 2002)	2002	Invertebrates	North America	Local	Combined with a species static model	No	A	No
(Meekins and McCarthy, 2002)	2002	Plants	North America	Local	Not combined with a species static model	No	P	No
(Johnson et al., 2001)	2001	Invertebrates	North America	Local	Not combined with a species static model	No	P	No
(Courchamp and Sugihara, 1999)	1999	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(Edwards et al., 1998)	1998	Plants	North America	Local	Not combined with a species static model	No	A	No
(Sharov and Liebhold, 1998b)	1998	Invertebrates	North America	Local	Not combined with a species static model	No	A	No
(Sharov and Liebhold, 1998a)	1998	Invertebrates	North America	Regional	Not combined with a species static model	No	A	Yes
(Lampo and De Leo, 1998)	1998	Vertebrates	Oceania	no reference	Not combined with a species static model	No	A	No
(Schreiber and Gutierrez, 1998)	1998	Not specified	No reference	no reference	Not combined with a species static model	No	A	No

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Sharov et al., 1998)	1998	Invertebrates	North America	Local	Not combined with a species static model	No	A, P	Yes
(Gutierrez and Ponti, 2014)	2014	Plants	North America	Local	Not combined with a species static model	Yes	A, P	No
(Russell et al., 2014)	2014	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(Lampert et al., 2014)	2014	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Xu et al., 2014)	2014	Not specified	Global	Global	Combined with a species static model	Yes	P	No
(Robinson et al., 2013)	2013	Vertebrates	North America	Regional	Not combined with a species static model	No	P	No
(Amodeo and Zalba, 2013)	2013	Plants	Other	Local	Not combined with a species static model	No	P	No
(Calviño-Cancela and Rubido-Bará, 2013)	2013	Plants	Europe	Local	Not combined with a species static model	No	P	No
(Johnston and Purkis, 2013)	2013	Vertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Petrosyan et al., 2013)	2013	Vertebrates	Other	Local	Not combined with a species static model	No	P	No
(Matlaga and Davis, 2013)	2013	Plants	North America	Local	Not combined with a species static model	No	P	No
(Creutzburg et al., 2012)	2012	Plants	North America	Local	Combined with a species static model	Yes	P	No
(Lindgren and Walker, 2012)	2012	Plants	North America	Local	Combined with a species static model	Yes	P	No
(Sester et al., 2012)	2012	Plants	Europe	Local	Not combined with a species static model	Yes	A	No
(Lessa and Bergallo, 2012)	2012	Vertebrates	Other	Local	Not combined with a species static model	No	A	No
(Mercader et al., 2012)	2012	Invertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Parshad, 2011)	2011	Vertebrates	No reference	no reference	Not combined with a species static model	No	A	No
(Hatala et al., 2011)	2011	Other taxa	North America	Local	Not combined with a species static model	No	P	No
(James et al., 2011)	2011	Plants	Oceania	Local	Not combined with a species static model	No	A	No
(Richardson et al., 2010)	2010	Plants	Other	Regional	Combined with a species static model	Yes	A	No
(Yemshanov et al., 2010a)	2010	Invertebrates	North America	Local	Not combined with a species static model	Yes	P	No
(Ursino, 2010)	2010	Plants	No reference	Local	Not combined with a species static model	Yes	A	No
(Morris Jr et al., 2010)	2010	Vertebrates	Other	no reference	Not combined with a species static model	No	A	No
(Fenichel et al., 2010)	2010	Other taxa	No reference	no reference	Not combined with a species static model	No	A	Yes
(Renton, 2009)	2009	Plants	No reference	no reference	Not combined with a species static model	No	A	No
(Pardini et al., 2009)	2009	Plants	North America	Local	Not combined with a species static model	No	A	No
(Hoofman et al., 2008)	2008	Plants	No reference	no reference	Not combined with a species static model	No	P	No
(Mata-González et al., 2008)	2008	Plants	North America	Local	Not combined with a species static model	Yes	A	No
(Baxter et al., 2008)	2008	Not specified	No reference	no reference	Not combined with a species static model	No	A	Yes

Reference	Year	Taxonomical focus	Geographical focus	Spatial extent	Modelling framework	Model spatial explicitly	Management option	Cost evaluation
(Hüls et al., 2007)	2007	Plants	Europe	Local	Not combined with a species static model	No	A	No
(Wiedner et al., 2007)	2007	Other taxa	Europe	Local	Not combined with a species static model	No	P	No
(Nehrbass and Winkler, 2007)	2007	Plants	Europe	Local	Not combined with a species static model	Yes	P	No
(Daraio et al., 2006)	2006	Invertebrates	North America	Local	Combined with a species static model	Yes	P	No
(Shea et al., 2006)	2006	Plants	Oceania	no reference	Not combined with a species static model	No	A	No
(Hyatt and Araki, 2006)	2006	Plants	North America	Local	Not combined with a species static model	No	A	No
(Goslee et al., 2006)	2006	Plants	North America	Local	Not combined with a species static model	Yes	P	No
(Rinella and Sheley, 2005a)	2005	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Rinella and Sheley, 2005b)	2005	Plants	North America	Local	Not combined with a species static model	No	A	Yes
(Drake, 2005b)	2005	Vertebrates	North America	Local	Not combined with a species static model	No	P	No
(Magda et al., 2004)	2004	Plants	Europe	Local	Not combined with a species static model	No	A	No
(Pratt et al., 2004)	2004	Plants	North America	Local	Not combined with a species static model	No	A	No
(Brook et al., 2003)	2003	Vertebrates	Other	Regional	Not combined with a species static model	No	A	No
(Barlow and Choquenot, 2002)	2002	Vertebrates	Oceania	no reference	Not combined with a species static model	No	P	No
(Buckley et al., 2001)	2001	Plants	Europe	Local	Not combined with a species static model	No	A	No
(Parker, 2000)	2000	Plants	North America	Local	Not combined with a species static model	No	A	No
(Kean and Barlow, 2000)	2000	Not specified	No reference	no reference	Not combined with a species static model	No	A	No
(Crawley, 1987)	1987	Not specified	No reference	no reference	Not combined with a species static model	No	P	No
(Santulli et al., 2014)	2014	Vertebrates	Europe	Local	Not combined with a species static model	Yes	A	No
(Gorchov et al., 2014)	2014	Plants	North America	Local	Not combined with a species static model	No	P	No
(Castellanos-Frías et al., 2014)	2014	Plants	Europe	Regional	Combined with a species static model	Yes	P	No
(Burgman et al., 2013)	2013	Other taxa	Oceania	Local	Combined with a species static model	Yes	P	No
(Batabyal and Nijkamp, 2005)	2005	Not specified	No reference	no reference	Not combined with a species static model	No	P	Yes

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